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Volume 113
Number 3
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Contents

Articles

231–241 **Parrish, Frank A., Nicholas T. Hayman, Christopher Kelley, and Raymond C. Boland**

Acoustic tagging and monitoring of cultured and wild juvenile crimson jobfish (*Pristipomoides filamentosus*) in a nursery habitat

242–255 **Dahlheim, Marilyn E., Alexandre N. Zerbini, Janice M. Waite, and Amy S. Kennedy**

Temporal changes in abundance of harbor porpoise (*Phocoena phocoena*) inhabiting the inland waters of Southeast Alaska

256–269 **Ryer, Clifford H., William C. Long, Mara L. Spencer, and Paul Iseri**

Depth distribution, habitat associations, and differential growth of newly settled southern Tanner crab (*Chionoecetes bairdi*) in embayments around Kodiak Island, Alaska

270-289 **Edward A. Laman, Stan Kotwicki, and Christopher N. Rooper**

Correlating environmental and biogenic factors with abundance and distribution of Pacific ocean perch (*Sebastes alutus*) in the Aleutian Islands, Alaska

290–301 **Willis, C. Michelle, Jonathan Richardson, Tracey Smart, Joseph Cowan, and Patrick Biondo**

Diet composition, feeding strategy, and diet overlap of 3 sciaenids along the southeastern United States

302–312 **Lin, Yu-Jia, Chi-Lu Sun, Yi-Jay Chang, and Wann-Nian Tzeng**

Sensitivity of yield-per-recruit and spawning-biomass-per-recruit models to bias and imprecision in life history parameters: an example based on life history parameters of Japanese eel (*Anguilla japonica*)

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313–326 **Nichol, Daniel G., and David A. Somerton**

Seasonal migrations of morphometrically mature male snow crab (*Chionoecetes opilio*) in the eastern Bering Sea in relation to mating dynamics

327–340 **Beck, Steve, and Megan K. La Peyre**

Effects of oyster harvest activities on Louisiana reef habitat and resident nekton communities

341–351 **O'Farrell, Michael R., and William H. Satterthwaite**

Inferred historical fishing mortality rates for an endangered population of Chinook salmon (*Onchorhynchus tshawytscha*)

352–354 **Guidelines for authors**

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First U.S. Commissioner
of Fisheries and founder
of *Fishery Bulletin*

Acoustic tagging and monitoring of cultured and wild juvenile crimson jobfish (*Pristipomoides filamentosus*) in a nursery habitat

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Abstract—The movements of cultured (n=18) and wild (n=28) juvenile crimson jobfish (*Pristipomoides filamentosus*) are reported for a known nursery off windward Oahu, Hawaii. The 2 batches of fish were tagged with acoustic transmitters in separate years (2006, 2007) and monitored with a receiver array for up to 10 weeks. Of the cultured fish, 75% left the nursery within 3 days, more than twice the exit rate for wild fish tagged the following year. The number of wild fish detected peaked during daylight hours, indicating that the fish were diurnally active. Tidally driven changes in bottom temperature did not explain the behavioral patterns of the wild fish that remained in the nursery for multiple weeks. Additional receivers deployed on the slope adjacent to the nursery detected that two-thirds of the wild fish departed from the nursery after a short period (mean: 1.2 days [SD 1.69]), by crossing areas with soft substrate similar to that of the nursery. In contrast, the fish that exited by rock ledges stayed near the rock ledges longer (mean: 13.3 days [SD 20.9]). These movement patterns provide insight into the early life history of this deepwater snapper and a glimpse at some of the challenges for future stock enhancement efforts.

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Eteline snappers compose an important, high-value component of tropical insular fisheries throughout the Pacific and Indian Oceans, and catch of sizeable portions is exported from their country or archipelago of origin. The crimson jobfish (*Pristipomoides filamentosus*), also known as the pink snapper, composes more than a quarter of the commercial landings by weight of the Hawaiian bottomfish fishery (Brodziak et al., 2011). In addition, this species is thought to account for roughly the same percentage of bottomfish recreational landings, which, when added to commercial landings, would increase the overall catch of this snapper by a factor of 2–3 (Zeller et al., 2008). Because of the high market value of crimson jobfish, scientists of the University of Hawaii spent a considerable effort during 1997–2006 attempting to breed this species in captivity for potential use in aquaculture and stock enhancement. They were successful at maintaining broodstock, producing larvae, and rearing fish to 20–24 cm in fork length (FL) (C. Kelley, unpubl. data), which is similar to the size of juveniles that occur in nearshore nursery habitats.

Culturing large numbers of juveniles is not yet possible, but if it is achieved, they hypothetically could be grown for harvest in oceanic cages or used to enhance wild populations through releases to known nursery grounds as is done with other fisheries species (Bell et al., 2008). Although these types of enhancement activities have been undertaken for freshwater and anadromous species, their use in marine systems is more recent. Notable examples in Hawaii include hatchery releases of striped mullet (*Mugil cephalus*) (Leber and Arce, 1996) and Pacific threadfin (*Polydactylus sexfilis*) (Friedlander and Ziemann, 2003).

In order to release cultured fish into the wild for the purposes of stock enhancement, researchers will need to know where to deploy the fish and how they will behave. Ideally, cultured juvenile fish would be released in a place suitable for that stage of its life history. Larvae of eteline lutjanid snappers are known to reside in the plankton until they

reach a length of 5–6 cm FL (Leis, 1987; Leis and Lee, 1994). Crimson jobfish settle and form loose schools over featureless soft-bottom habitat at depths of 80–100 m (Parrish, 1989). While in their nursery they feed on benthic and, to a lesser extent, a mix of planktonic invertebrates and small nektonic fishes (DeMartini et al., 1996; Schumacher, 2011). Survey results indicate that slope areas close to sources of coastal discharge (e.g., draining embayments or reef channels) tend to support greater numbers of juveniles and serve as premium habitat or nursery grounds (Parrish et al., 1997). These nurseries are important gateways in the life history of the crimson jobfish and provide a window to understanding and predicting year-class fluctuations.

The most studied nursery ground for crimson jobfish in Hawaii is the offshore area of Kaneohe Bay, Oahu. Monthly sampling of the juvenile population in this area has revealed seasonal patterns in the distribution of fish sizes consistent with an annual progression of a year class through its recruitment, growth, and emigration to adult habitats (Moffitt and Parrish, 1996). Fish at sizes of 7–10 cm FL appear in this nursery habitat in the fall and stay there for a period of 6–7 months until they reach 20–30 cm FL (Moffitt and Parrish, 1996). Otolith features of juvenile crimson jobfish indicate ages of ~6 months for 10.5-cm-FL fish, about a year for 18.5-cm-FL fish, and 2 and 3 years, respectively, for 28.0- and 36.0-cm-FL fish (DeMartini et al., 1994; Andrews et al., 2012). At 2–3 years of age, fish begin to emigrate offshore to deeper habitats used by subadults (Okamoto[1]) and adults (Haight et al., 1993a). Because only 2 wild juvenile crimson jobfish had been tagged and tracked in the Kaneohe nursery (Moffitt and Parrish, 1996) before our study, there has been insufficient understanding of juvenile crimson jobfish movements and how they might compare with those of crimson jobfish raised in captivity.

In this study, we report new observations of 2 batches of juvenile crimson jobfish that were implanted with acoustic tags and released in separate years to the nursery habitat off windward Oahu. In the first year (2006) of this study, a batch of cultured fish were tagged and released, followed by a second year (2007) in which wild fish were collected from the nursery, tagged, held for observation, and then released. We investigated the hypotheses that cultured juvenile fish released to a known nursery site would linger and make use of the nursery habitat or move directly off to other locations. Similarly, we investigated whether the wild fish taken from the site, tagged, and released back to the nursery would behave differently from the cultured fish.

[1] Okamoto, H. Y. 1993. Project to develop opakapaka (pink snapper) tagging technique to assess movement behavior. Final Report of the Hawaii Department of Land and Natural Resources to NOAA, 18 p. NOAA Award No. NA90AA-D-IJ466. [Available from Division of Aquatic Resources, Hawaii Department of Land and Natural Resources, 1151 Punchbowl Street, Room 330, Honolulu, HI 96813-3088.]

Materials and methods

Study area

The Kaneohe Bay nursery (Fig. 1) is a submerged terrace, 70–100 m deep, roughly 8 km2 in area, and is separated from the nearest known aggregation of adult crimson jobfish by more than 5 km. Video surveys (Parrish et al., 1997), backscatter data collected with a multibeam sonar (Dartnell and Gardner[2]), and sidescan sonar data (C. Kelley, unpubl. data) indicate that the bottom at this nursery site is "soft" (unconsolidated sediment) and generally featureless. Two isolated, exposed rock ledges identified on the slope adjacent to the nursery were hypothesized to be potential transition habitats for juveniles when they leave the nursery to emigrate to deeper, hardbottom adult habitat.

Receivers

We monitored the nursery ground with two VR2[3] passive underwater receivers (VEMCO, Bedford, Canada), deployed in 2006 approximately 800 m apart at a depth of 75–80 m. Subsurface floats suspended the receivers 5 m above the bottom to maximize reception of signals from tagged fish. This configuration reduced acoustic effects on signal reception from the thermocline (Siderius et al., 2007). Weighted with a concrete anchor, the receivers were fitted with an ORE Offshore SWR acoustic release transponder (EdgeTech, West Wareham, MA) that detached and allowed the receivers to float to the surface when a coded acoustic signal was transmitted. In 2007, 4 additional receivers were deployed at a depth of 140 m at sites on the adjacent slope (2 north and 2 south of the nursery), and each pair was split between soft bottom (sites 2 and 4) and rock ledge (sites 1 and 3) habitats (Fig. 1). The receivers on the slope were separated from other receivers by distances ranging from 1200 to 2500 m. Attached to the bottom of each receiver mooring, a temperature data logger recorded temperatures on an hourly basis to track tidal effects of a cold bottom layer that had been identified at the Kaneohe nursery in previous studies (Moffitt and Parrish, 1996).

Tagging of juvenile fish

Cultured juveniles were raised in captivity from eggs spawned from broodstock held at the Hawaii Institute of Marine Biology (HIMB), a marine research center of the University of Hawaii at Manoa located on Co-

[2] Dartnell, P., and J. V. Gardner. 1999. Sea-floor images and data from multibeam surveys in San Francisco Bay, Southern California, Hawaii, the Gulf of Mexico, and Lake Tahoe, California-Nevada. U.S. Geological Survey Digital Data Series DDS-55, vers. 1.0. [Online version of interactive CD-ROM. Available at Website.]

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

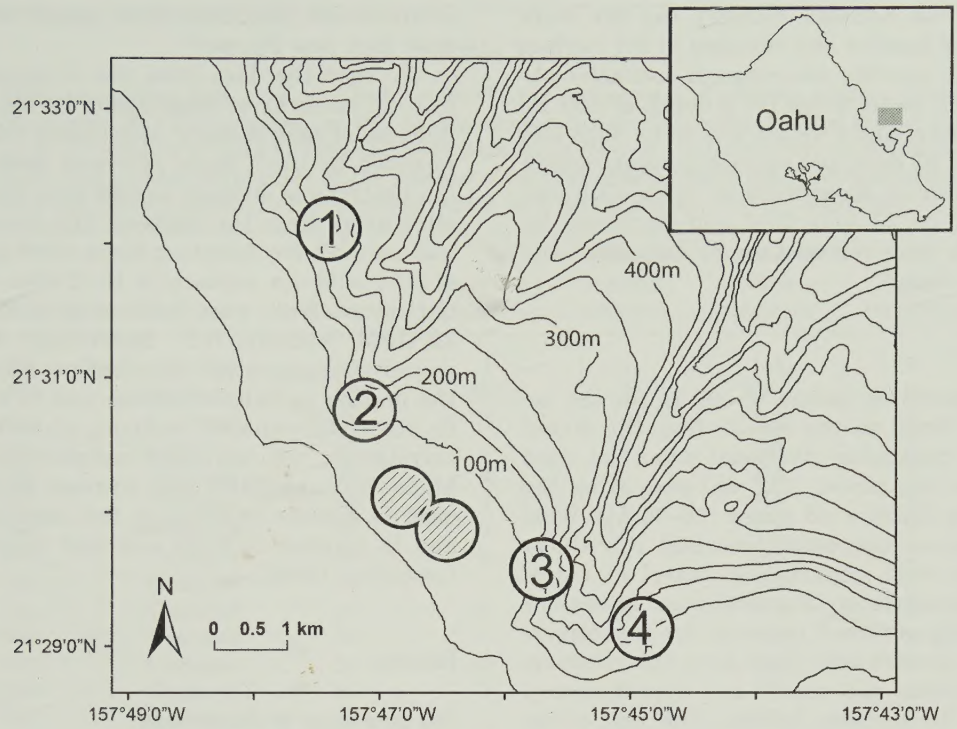

Figure 1

Map of the study area off windward Oahu, showing the deployment sites of 6 receivers with their 400-m radiuses of detection. The gray rectangle in the inset map indicates the position of the study area off the island of Oahu. Two receivers, the locations of which are indicated by the circles filled with diagonal lines, monitored movements of tagged juvenile crimson jobfish (*Pristipomoides filamentosus*) in the snapper nursery on a terrace outside of Kaneohe Bay where tagged cultured and wild crimson jobfish were released in 2006 and 2007, respectively. Open circles indicate the sites (numbered 1–4) where additional receivers were deployed in 2007 to monitor the use by the tagged wild fish of rock ledge (sites 1 and 4) and soft bottom (sites 2 and 4) habitats on the slope adjacent to the nursery. Lines indicate depth contours in meters.

conut Island in Kaneohe Bay. Broodstock juveniles were originally captured from the Kaneohe nursery and raised through sexual maturity in floating pens. Spawned eggs were collected from the broodstock pens and transferred to tanks in a fish hatchery facility at HIMB. Larvae were raised in tanks for 4 months, then transferred to floating pens where rearing continued until they were 8 months of age and had grown to 20–24 cm FL, a considerably faster growth rate than those reported for wild fish and based on otolith analyses (DeMartini et al., 1994; Andrews et al., 2012). The acoustic tags were surgically implanted, and the fish were held in a floating pen for 4 days to verify that they continued to swim and feed actively.

Wild juveniles (17–30 cm FL) were collected from the Kaneohe nursery by hook and line, verified as crimson jobfish (Uchida and Uchiyama, 1986), implanted with acoustic tags, and observed in a floating holding pen for 10 days until ocean conditions permitted transport of fish to the nursery site for release. Two fish died, the first within an hour of surgery and the second that evening. All other fish schooled and fed normally during days of observation.

The tags were V9 transmitters (VEMCO; 69 kHz, 9 by 21 mm), each of which had a unique code, was sterilized with alcohol, and inserted into the ventral abdominal cavity of a fish through a 1-cm incision while that fish was anesthetized in a bath of tricaine methanesulfonate (Finquel MS-222, Argent Chemical Laboratories, Redmond, WA). Iodine and binding tissue adhesive were applied to the wound, and it was closed with a square knot suture made with a 2.0 surgical needle. To minimize handling, the lengths of both cultured and wild fish were measured in the water and the percentage of tag weight to body weight was estimated by using a published length-weight relationship for juvenile crimson jobfish (n=125) collected from the study area (Moffitt and Parrish, 1996). In the sample of fish tagged, the tags never exceeded 4% of the body weight (Brown et al., 1999).

On the day of release, we used a receiver to confirm that the tag in each fish was functioning and transmit-

ting a signal. At the Kaneohe nursery, the fish were split equally into 2 batches and released at the surface over each of the 2 receiver moorings. A snorkeler observed that all fish swam down (to a depth of ~30 m) and disappeared from sight within a minute. Tags had an expected life of 95 days and emitted a signal with a pseudorandom delay at an average of 100 s. Cultured fish were released on 23 June 2006 and monitored for 58 days; wild fish were released on 10 July 2007 and monitored for 76 days.

Data analysis

We assumed a detection radius of 400 m for the receivers that was based on the results from the manufacturer's range calculator (Website) when we used the inputs of the tag power (151 db) and using the average windward Oahu wind speed (15–20 kt). Wind speed affects sea-surface conditions and introduces background noise that impacts the travel of transmitter signals underwater. Simultaneous detections were rare and only occurred between the 2 receivers deployed on the nursery site; they were the receivers closest to each other and monitored approximately half the area of the nursery habitat. The rest of the receivers allowed us to monitor habitat on the slope and were spaced far enough apart to avoid overlapping detections. It was necessary to discern signals from a tag on a resident, live fish from signals from a tag that was still transmitting but lost on the bottom for various reasons (e.g., tag expulsion or death of fish). For the purposes of this study, signals were assumed to be emitted from dead fish if 1) they had an inordinately high number of detections (e.g., >15,000) consistent with the detection of the continuous transmitting of a tag lost on the bottom for the full duration of the surveillance period and 2) they were detected by only 1 receiver.

Because prior tracking (Moffitt and Parrish, 1996) indicated that movement patterns of fish in the nursery differed between day and night, the detections of the fish in our study were binned in 6-h intervals for analysis (2400–0559, 0600–1159, 1200–1759, and 1800–2359). Initially, the density of tagged fish (and the risk of signal collisions) was high; therefore, we required 2 or more successive signals detected within 1 h to provide greater temporal resolution for the first 3 days. We defined a signal as "successive" if it was a repeat signal detected within 5 min of the previous signal—a time period adequate enough for 2 detections given the cycle of the tag's delay between transmissions. After 3 days, when most of the fish had departed, the risk of signal collisions that create false detections was reduced; therefore, multiple (>2) isolated detections (spaced more than 5 min apart) were accepted as long as they fell within the 6-h time interval. Combining successive detections binned by time intervals increased confidence that the fish were actually present (94.5% confidence intervals binned by hour, 97.9% by 6 h) and rendered insignificant the effect on our analysis of erroneous detections from signal collisions of multiple tags (see Pincock[4]).

We used the data from the 2 nursery receivers to look at patterns of time spent in the nursery, of influences of temperature, and of fish body length. Data recorded by the 4 slope receivers were used to examine patterns of habitat use by wild fish as they travelled away from the nursery. The sample size of fish was suitable for detecting large effect sizes at a power of 0.80 with an alpha of 0.10 (Cohen, 1988). All statistical analyses were performed in IBM SPSS, vers. 22 (IBM, Armonk, NY). Normalized data fitted to a negative exponential distribution showed how close the decline in fish detections was to a constant rate. In other comparisons, analysis of variance (ANOVA), correlation, and standard nonparametric tests (e.g., Mann-Whitney [MW] and Kruskal-Wallis [KW]) were used to analyze patterns in fish movements over time and in relation to body size and habitat (Siegel and Castellan, 1988).

Results

Tag detections in the nursery

Movements documented through tag detections indicated that 18 cultured fish and 28 wild fish were alive and suitable for inclusion in the analysis (Table 1). Seven other fish were excluded, including 2 wild fish that went undetected, 2 wild fish that were present only briefly (<10 signals), and 2 cultured and 1 wild fish whose tags emitted continuous signals recorded by 1 receiver (an indication that the tags were immobile and lying on the bottom because of tag expulsion or the death of a fish). Detections of tags lost on the bottom were unaffected by daily tidal changes in the temperature cycle, indicating that there was little effect from the thermocline on the reception of the receivers. Almost all (97%) of the tagged fish (cultured and wild) used in the analysis moved back and forth between the 2 nursery receivers, indicating that the fish were active.

The signals of both cultured and wild fish declined exponentially to a low and variable level of presence by the end of the surveillance period in each year. Within 3 days of release, the portion of released cultured fish that were detected in the nursery area dropped to less than 20% in a pattern that closely fitted an inverse exponential curve (adjusted coefficient of multiple determination, R^2=0.821). In contrast, 75% of wild fish persisted in the nursery for 3 days, reducing the fit to the curve (adjusted R^2=0.205) and, therefore, indicating that the decline was not as continuous as the drop observed for cultured fish (Fig. 2).

[4] Pincock, D. G. 2012. False detections: what they are and how to remove them from detection data. Application note. AMIRIX Systems Inc. DOC-004691-03, 11 p. [Available at Website.]

Table 1

Fish tag number, fish type, and fork length (FL) in centimeters of juvenile crimson jobfish (*Pristipomoides filamentosus*), as well as the number of days they were detected during this study off windward Oahu in 2006 and 2007, number of receivers in the nursery that detected them, and number of receivers on the adjacent slope that detected these fish. The right column lists the figure numbers in this article in which each fish is plotted. NA=not applicable.

Fish tag	Fish type	FL (cm)	Duration (days)	Number of nursery receivers	Number of slope receivers	Figure number(s)
691	Cultured	23	1	2	NA	2
692	Cultured	23	52	2	NA	2
693	Cultured	23	2	2	NA	2
695	Cultured	23	2	2	NA	2
696	Cultured	24	1	2	NA	2
697	Cultured	22	1	2	NA	2
698	Cultured	20	1	2	NA	2
699	Cultured	24	2	2	NA	2
700	Cultured	21	1	1	NA	2
701	Cultured	23	50	2	NA	2
702	Cultured	23	1	2	NA	2
703	Cultured	24	49	2	NA	2
704	Cultured	24	1	2	NA	2
705	Cultured	23	2	2	NA	2
706	Cultured	24	2	2	NA	2
708	Cultured	23	3	2	NA	2
709	Cultured	22	53	2	NA	2
710	Cultured	23	3	2	NA	2
1830	Wild	27	48	2	2	2, 3
1831	Wild	30	75	2	2	2, 3
1832	Wild	22	4	2	1	2, 3
1833	Wild	22	28	2	2	2, 3
1834	Wild	22	29	2	1	2, 3, 5
1835	Wild	19	75	2	0	2, 3, 5
1838	Wild	30	4	2	1	2, 3
1839	Wild	18	49	2	1	2, 3
1840	Wild	19	61	2	2	2, 3
1841	Wild	30	9	2	1	2, 3
1842	Wild	23	75	1	1	2, 3
1843	Wild	18	9	2	1	2, 3
1844	Wild	22	44	2	0	2, 3, 5
1847	Wild	17	5	1	1	2, 3
1848	Wild	26	5	2	1	2, 3
1849	Wild	30	74	2	2	2, 3
1850	Wild	18	60	2	2	2, 3, 5
1856	Wild	30	10	2	2	2, 3
1857	Wild	28	9	2	3	2, 3
1858	Wild	19	5	1	3	2, 3
1859	Wild	20	65	2	1	2, 3
1860	Wild	23	20	2	1	2, 3
1862	Wild	20	9	2	0	2, 3
1863	Wild	18	4	2	1	2, 3
1864	Wild	23	24	2	1	2, 3
1866	Wild	30	17	2	3	2, 3
1867	Wild	20	12	0	1	2, 3
1869	Wild	23	2	2	0	2, 3

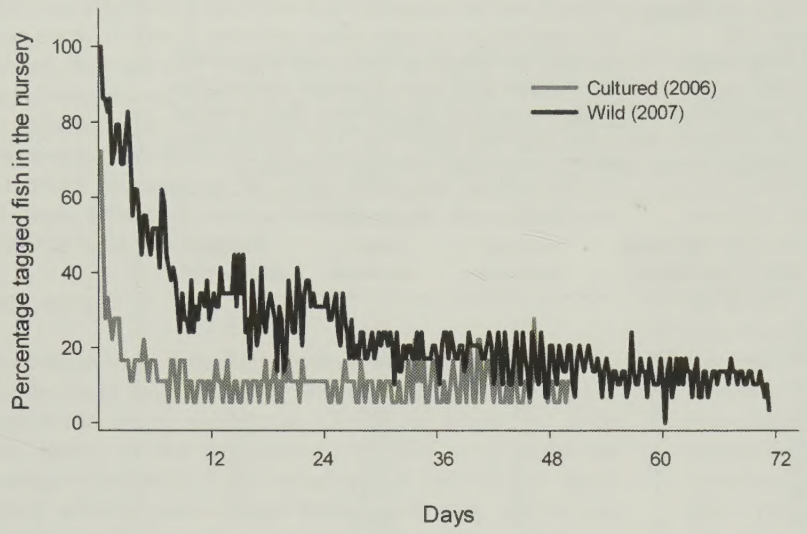

Figure 2

Percentage of cultured and wild juvenile crimson jobfish (*Pristipomoides filamentosus*) detected with acoustic telemetry over time after their release in the nursery offshore of Kaneohe Bay, windward Oahu, in 2006 and 2007, respectively, to observe their movements.

The mean fork lengths of the 2 groups were similar (cultured: 22.3 cm [SD 1.0]; wild: 23.1 cm [SD 4.5]), but the range was greater for wild fish. However, even in an analysis where the sample of wild fish was limited in relation to fish in the narrower size range of cultured fish (20–24 cm FL), the wild fish still persisted in the nursery significantly longer than cultured fish (MW: Z=–2.6, P<0.01). Comparison of the body lengths of all wild fish according to time spent in the nursery showed that bigger fish left sooner (coefficient of correlation, r=–0.39, n=28, P<0.05).

Light and temperature

The wild fish lingered in the nursery for 3 days after release, and documented movements indicate a bimodal pattern of higher numbers of the wild fish in the nursery during the day than during the night, indicating that the fish were diurnally active (Fig. 3). The inflection point in the pattern of data for high and low fish numbers was most obvious around dawn and dusk and the larger daytime numbers were statistically significant (ANOVA: F=23.7, P<0.001). In the evening, when detections in the nursery were lower, there was no corresponding increase in the number of fish detected at the receivers on the slope adjacent to the nursery (t=–0.57, P=0.572)

The tidally driven cycle of bottom temperature in the nursery is another variable that potentially could influence fish behavior. Prior work has shown that high tides pushed a cooler, bottom-associated lens of water (~2°C colder) into the nursery (Moffitt and Parrish, 1996). Our data loggers on the bottom confirmed this tidal influx of cold water for both years with the temperature cycle ranging between 22.0°C and 25.5°C (Fig. 4). This prominent environmental feature is present interannually, but the cyclical change in temperature did not appear to control the behavior of the fish in our study. Tag detections indicate that 4 of the wild crimson jobfish (18–22 cm FL) stayed at the nursery for multiple weeks, and, during that time, they showed no behavioral change attributable to the temperature cycle (Fig. 5). One of those wild fish (tag 1835) moved from the range of one receiver on the terrace to the other receiver and then adopted a pattern of being present during the day and absent at night. Movements of the other 3 fish (tags 1834, 1850, and 1844) showed that they remained continuously within the range of detection for large portions of the period regardless of changes in temperature.

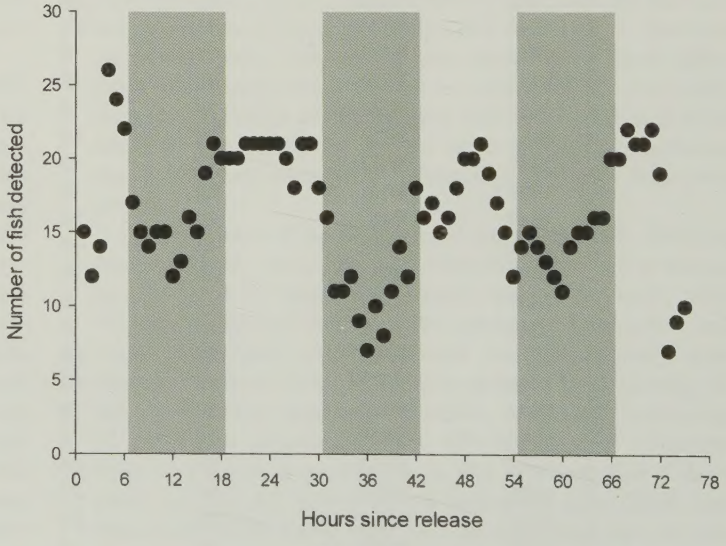

Figure 3

Bimodal pattern in the numbers of wild juvenile crimson jobfish (*Pristipomoides filamentosus*) detected by hour for the first 3 days after release in 2007 of fish in the nursery offshore of Kaneohe Bay, windward Oahu. The gray bars represent hours of night.

Wild fish movements on the slope

One or more of the 4 slope receivers was visited by 85% of the wild fish. Some fish passed them briefly, as they emigrated away from the nursery into deeper waters, and others chose to linger on the slope for a while before moving deeper. All the receivers were visited, but more than half the tagged fish visited the slope receiver closest to the nursery (located at site 2 north of the nursery; Fig. 1) (Table 2). There was no significant difference in the number of fish visiting soft bottom versus rock ledge habitats (MW: Z=–1.3, P=0.21). The number of days the fish lingered at the slope sites varied widely because of their habitat type and distance from the nursery; however, a mixed-effects model showed that the longest stays were at the sites with rock ledges (sites 1 and 3; Fig. 1) (F=4.99, P=0.012). The range of fish lengths (18–30 cm FL) did not significantly differ between substrate types (MW: Z=–0.172, P=0.88). Temperatures at the 4 slope receivers were on average 2°C cooler (Table 2) than the temperatures at the 2 receivers in the nursery. Only at slope site 3, located to the south of the nursery close to the head of a deep canyon, were average temperatures nearly 1°C cooler than the average temperatures at the locations of other slope receivers (KW: $\chi 2$=633, P<0.001). The receiver at site 3 recorded 3 of the 4 fish with the longest stays on the slope (28–61 days). The fourth fish had the maximum stay (8 days) near the receivers deployed in soft bottom habitats (sites 2 and 4), after it had spent 23 days at the northern rock ledge habitat (site 1).

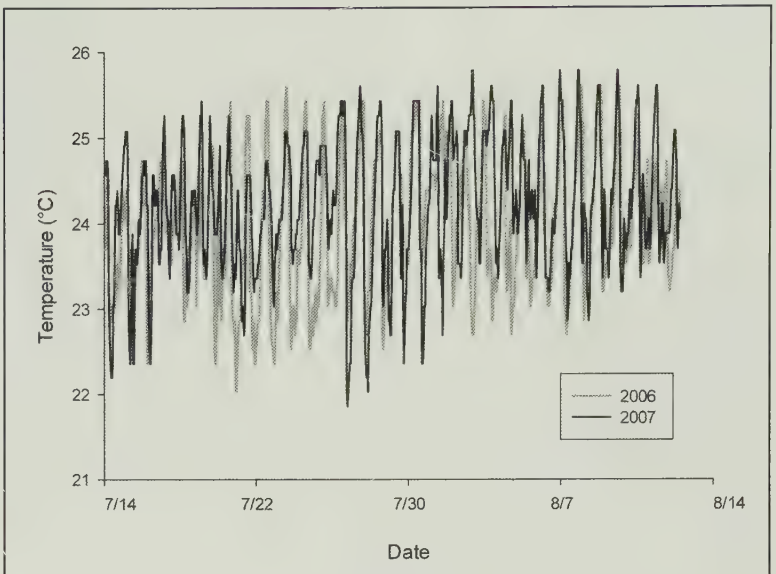

Figure 4

Bottom temperatures in degrees Celsius recorded over the same period at the sites off windward Oahu where crimson jobfish (*Pristipomoides filamentosus*) were released in 2006 (cultured fish) and in 2007 (wild fish), showing similar tidally driven fluctuations between 22.0°C and 25.5°C in both years.

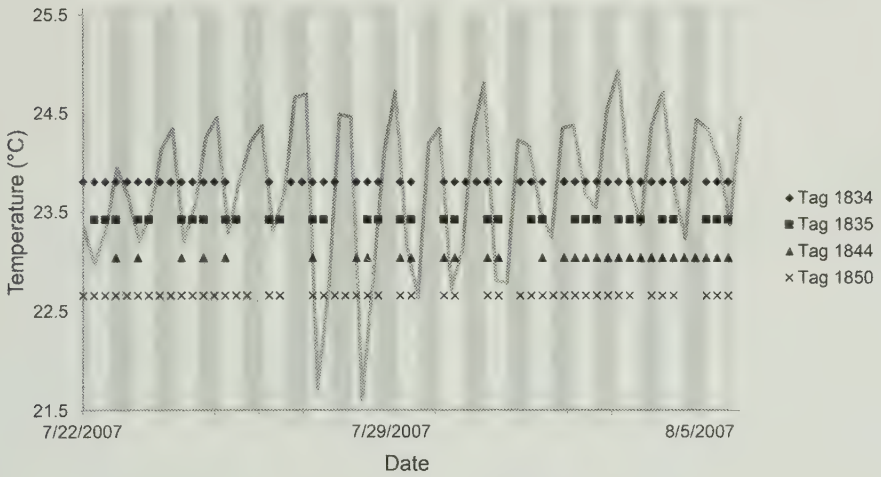

Figure 5

The diverse set of presence and absence patterns for 4 individual juvenile crimson jobfish (*Pristipomoides filamentosus*). Detections of their tags were binned by periods of 6 h, that persisted at the nursery offshore of Kaneohe Bay, windward Oahu, for a 15-day period in 2007. The gray bars represent hours of night, and the gray line is the bottom temperature in degrees Celsius.

Discussion

Time in the nursery

It is unknown why the signals of cultured fish released in the first year of this study disappeared faster than wild fish in the second year. This release is the first one of a deepwater fish species raised in captivity. There are many potential factors, such as depth, light levels, and temperature, that likely influenced the behavior of the released cultured fish. Cultured fish reared in the warm surface water of a bay cage had none of the familiarity with the nursery habitat that the wild fish had. The released wild fish lingered because they knew the site, they had not yet matured enough to emigrate, or there were significant environmental differences between years that influenced fish behavior.

Environmental effects, including freshwater discharge, have been reported to influence the behavior of tagged marine species in coastal estuaries during their early life history (Manderson et al., 2014). The Kaneohe nursery differs from nurseries in estuarine habitats, because it is located deep, at the edge of an oceanic slope, where the substrate, temperature (Moffitt and Parrish, 1996), and nutrients (Parrish et al., 1997) have been found to be consistent between years in prior studies. The temperature records from both tagging years in this study were similar, and there is no clear association between temperature and behavior of the crimson jobfish. The original plan was to conduct a simultaneous release of cultured and wild fish in 2007 to compare their behavior, but the funding for the culture program was unexpectedly cut. Future studies are needed to distinguish whether interannual environmental effects are indeed a concern or whether the observed fish behavior is due to the inability (or a lack of need) for cultured juvenile fish to integrate into an assemblage of wild juveniles.

Potential tagging effects

Surgical implantation of acoustic tags in small fish has the potential to add significant weight and affect the fish's buoyancy and behavior. Prior studies (McCleave and Stred, 1975; Adams et al., 1998) recommended that tags should be no more than 2% of fish body weight. The V9 tags exceeded this percentage for 8 of our fish; 1 tag in 1 fish accounted for as high as 3.3% of estimated body weight. However, all the fish fell well within the percentage of tag weight identified by Brown et al. (1999), who showed success with the use of tags that were 6–12% of body mass of juvenile salmon (smolt). Our observations of fish actively swimming in the holding pen for days before release and documented movement between receivers after release indicate that there was little behavioral effect from the size of the tags used.

Having endured the stress of tagging, release, and descent through the water column, most of the released fish successfully reached the bottom where they were repeatedly detected for a day or more by the nursery receivers. A single 20-cm fish (tag 1867) was not detected by either of the nursery receivers after it was released, but it appeared 9 days later at site 3 on the adjacent slope (Fig 1). It stayed there for 2 days before disappearing from the study. The disappearance of tag signals is either the result of the fish emigrating outside the receiver surveillance area or of it being consumed by a predator that leaves the area. The featureless mud bottom of the nursery supports few other fish (DeMartini et al., 1996) that would be resident predators of the crimson jobfish; therefore, predation loss was likely from larger, transient fishes that passed through the nursery. Loss of tagged fish to predation is expected, although we have no way to evaluate the degree of this impact.

Movement of wild fish

There have been few studies of tagged deepwater snappers and most of them have been of adult fish. The most recent work (Weng, 2013) looked at movements of tagged adult eteline red snappers and found that ruby snapper (*Etelis carbunculus*) showed more fidelity to the area of their release than did tagged flame snapper (*Etelis coruscans*). A separate study of 18 tagged adult crimson jobfish (40–60 cm FL) showed that 75% of fish remained in the monitored release area (Ziemann and Kelley[5]). Because those mature fish had already immigrated to their adult habitat, we might expect greater fidelity for them than for the juvenile fish in our study. In contrast, we examined the temporary use of nursery habitat by juveniles before they moved to the next stage in their life history.

The time spent in the nursery varied from a few days to multiple weeks. For many of the fish tagged in our study, diurnal movements were detected in and out of the range of receivers in the nursery. The study on tagged adult crimson jobfish found that they aggregated during the day and ranged over a wider area at night (Ziemann and Kelley[5]). The movements of the juveniles in our study were much more limited. The receivers deployed on the slope adjacent to the nursery did not detect a greater number of juvenile crimson jobfish during evening hours than during daytime hours; an increase would be expected if the fish were engaged in wide-ranging movements. It is possible that the juveniles could have moved inshore to shallower depths; however, data from a previous study that conducted boat-based tracking of 2 juveniles indicated that the fish would move deeper (Moffitt and Parrish, 1996). The individual tracks of both fish showed crepuscular movements, the fish stayed in shallower wa-

[5] Ziemann, D., and C. Kelley. 2004. Detection and documentation of bottomfish spillover from the Kaho'olawe Island Reserve. Final report submitted to the Kaho'olawe Island Reserve Commission for Study I. [Available from Kaho'olawe Island Reserve Commission, 811 Kolo St., Ste. 201, Wailuku, HI 96793.]

Table 2

The identification number and substrate type of the 4 sites on the windward Oahu slope where receivers were deployed in 2007. Also shown is the distance in kilometers of each receiver from the nursery, number of tagged juvenile crimson jobfish (Pristipomoides filamentosus) that were detected, mean number of days when those fish were present at each site, and mean bottom temperature at each site. For "Days present" the mean, standard deviation (SD), and range are given for each site. There were 2 substrate types: rock ledge and soft bottom.

				Days present		Temp. (°C)
Receiver	Substrate	Nursery (km)	No. fish	Mean (SD)	Range	Mean (SD)
1	Rock	4.0	5	6.0 (9.9)	0.25–23.5	21.8 (1.0)
2	Soft	1.5	17	1.5 (2.0)	0.25–8.3	21.8 (1.0)
3	Rock	1.8	8	17.8 (25.2)	0.25–61.0	21.0 (1.0)
4	Soft	3.3	8	0.6 (0.4)	0.25–2.0	21.8 (1.0)

ter during the day and in deeper water at night, shifting between adjacent areas (<300 m separation) that differed slightly in depth (~10 m). For both tracks, the area of daytime activity was twice the size of the area of activity at night.

This commuting behavior could explain the bimodal pattern seen for the tagged fish in our study before they left the nursery. If these fish also shifted deeper at night, some of them would be out of detection range until morning when they returned to the shallower portion of their home range and were more active. Looking at the patterns in the movements of the 4 wild fish that persisted in the nursery for multiple weeks, 2 fish (tags 1834 and 1850) appeared to have both their areas of activity during day and night mostly inside the detection area of the receivers in the nursery (Fig. 5). In contrast, the pattern of a third fish (tag 1835) indicates that the area of activity during the day was within the detection range of the receiver and the area of nighttime activity was outside that range. Some drift in the home range of individual fish can occur, as was observed for the fourth wild fish (tag 1844) that stayed at the nursery for multiple weeks, but the extent to which the size or location of home ranges are subject to change over time is unknown.

As the wild fish departed the nursery and ranged farther out on the slope, they used both soft bottom and rock ledge habitats before emigrating away. Although the size of the fish at the sites on the slope did not statistically differ by habitat type of sites, a few of the larger fish (mean: 25.5 cm FL [SD 5.4]) clearly persisted for more than a month at sites with rock ledges. Crimson jobfish at this size are at the lower end of the size range of subadults documented to aggregate around relief features (Okamoto[1]). Presumably, this shift in habitat use occurs because the fish grow to a size where they need to change their diet or foraging strategy. Studies of stomach contents of crimson jobfish have shown a transition from a juvenile diet of mostly benthic invertebrates (DeMartini et al., 1996) to an adult diet of mostly large plankton, including jellies and salps (Haight et al., 1993b). Maturing and adult fish use high-relief habitat more than juveniles do—they exploit the increased water flow around relief features to improve their level of success in encountering and feeding on drifting plankton over their level of success at low-relief habitats. Future tagging work in the Kaneohe nursery should include receivers deployed in nearby locations with adult crimson jobfish assemblages to see if some of the emigrating juveniles make a direct transition to adult habitat.

Considerations for stock enhancement

Although we have no explanation for the behavioral difference seen between the 2 batches of tagged fish, the patterns observed for wild and cultured fish are similar to findings from other marine fish studies. Simultaneous releases of tagged cultured and wild individuals generally have shown that cultured fish tend to move away sooner and farther than wild fish (D'Anna et al., 2004; Yokota et al., 2007; Fairchild et al., 2009; Lino et al., 2009). Future studies with releases of tagged juvenile crimson jobfish might include a staged release process (Fairchild et al., 2010) that would give fish time to acclimate to the nursery and, therefore, make them more likely to use the habitat like wild fish. However, if cultured fish were to continue to leave the nursery directly, and there were no means to verify their survivorship after they have left, the use of larger fish (≥30 cm FL) that are old enough to skip the nursery stage and join subadults or adults should be considered for enhancement efforts. Stock enhancement studies on shallower Hawaiian species have shown that the size of release is an important variable in the success of stocking efforts (Leber, 1995; Leber et al., 1998; Leber et al., 2005). Finally, it is possible that being reared, or even just being held for a time in captivity and fed, can accelerate the ontogentic shift from the nursery stage to subadult phase in the life history of the crimson job-

fish. For example, the type or amount of food is likely to be better calorically in captivity than in the wild (Alasalvar et al., 2002; Gregorakis et al., 2002; Handeland et al., 2003; Periago et al., 2005; Benetti et al., 2010), and it could accelerate the development of the reserves a fish needs to graduate to the next habitat during its life history.

Within 3 days of release, the majority of tagged fish in both years departed from the nursery, although cultured fish exited at twice the rate of wild fish. There were no obvious environmental differences seen between years that could explain the different behavior patterns. For the batch of wild fish, higher numbers were detected during daylight hours than at night, and the movement of fish that stayed in the nursery for multiple weeks did not correspond with tidally driven changes in bottom temperature. Larger juveniles (>25 cm FL) emigrated away from the nursery earlier; two-thirds of these juveniles traveled across soft bottom habitats (mean: 1.2 days [SD 1.69]) and the rest lingered in areas with rock ledges (mean: 13.3 days [SD 20.9]). Our research indicates that juvenile crimson jobfish cultured in the laboratory or pulled from the wild will quickly emigrate even if released in a viable nursery habitat. This behavior prompts a number of ontogenetic, behavioral, and survivorship questions for future study that are particularly relevant for aquaculture as a means to enhance the stock of deep-slope fish species.

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Literature cited

Adams, N. S., D. W. Rondorf, S. D. Evans, and J. E. Kelly.
1998. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile Chinook salmon. Trans. Am. Fish. Soc. 127:128–136.

Alasalvar, C., K. D. A. Taylor, E. Zubcov, F. Shahidi, and M. Alexis.
2002. Differentiation of cultured and wild sea bass (*Dicentrarchus labrax*): total lipid content, fatty acid and trace mineral composition. Food Chem. 79:145–150.

Andrews A. H., E. E. DeMartini, J. Brodziak, R. S. Nichols, and R. L. Humphreys.
2012. A long-lived life history for a tropical, deepwater snapper (*Pristipomoides filamentosus*): bomb radiocarbon and lead–radium dating as extensions of daily increment analyses in otoliths. Can. J. Fish. Aquat. Sci. 69:1850–186

Bell, J. D., K. M. Leber, H. L. Blankenship, N. R. Loneragen, and R. Masuda.
2008. A new era for restocking, stock enhancement and sea ranching of coastal fisheries resources. Rev. Fish. Sci. 16:1–9.

Benetti, D. D., B. O'Hanlon, J. A. Rivera, A. W. Welch, C. Maxey, and M. R. Orhun.
2010. Growth rates of cobia (*Rachycentron canadum*) cultured in open ocean submerged cages in the Caribbean. Aquaculture 302:195–201.

Brodziak, J., D. Courtney, L Wagatsuma, J. O'Malley, H.-H. Lee, W. Walsh, A. Andrews, R. Humphreys, and G. DiNardo.
2011. Stock assessment of the main Hawaiian Islands Deep7 bottomfish complex through 2010. NOAA Tech. Memo., NOAA-TM-NMFS-PIFSC-29, 176 p.

Brown, R. S., S. J. Cooke, W. G. Anderson, and R. S. McKinley.
1999. Evidence to challenge the "2% rule" for biotelemetry. N. Am. J. Fish. Manage. 19:867–871.

Cohen, J.
1988. Statistical power analysis for the behavioral sciences 2nd ed., 567 p. Lawrence Erlbaum Associates, Hillsdale, NJ.

D'Anna G., V. M. Giacalone, F. Badalamenti, C. Pipitone.
2004. Releasing of hatchery-reared juveniles of the white seabream *Diplodus sargus* (L., 1758) in the Gulf of Castellammare artificial reef area (NW Sicily). Aquaculture 233:251–268.

DeMartini, E. E., K. C. Landgraf, and S. Ralston.
1994. A recharacterization of the age-length and growth relationships of Hawaiian snapper, *Pristipomoides filamentosus*. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-199, 14 p.

DeMartini, E. E., F. A. Parrish, and D. M. Ellis.
1996. Barotrauma-associated regurgitation of food: implications for diet studies of Hawaiian pink snapper *Pristipomoides filamentosus* (family Lutjanidae). Fish. Bull. 94:250–256.

Fairchild E. A., N. Rennels, and H. Howell.
2009. Using telemetry to monitor movements and habitat use of cultured and wild juvenile winter flounder in a shallow estuary. *In* Tagging and tracking of marine animals with electronic devices (J. L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage, and J. Sibert, eds.), Rev.: Methods Technol. Fish Biol. Fish. 9:5–22.

Fairchild E. A., J. A. Sulikowski, N. Rennels, W. H. Howell, and P. C. W. Tsang.
2010. Effects of moving acclimation cages before release of cultured fish: alternate release strategies for a juvenile winter flounder *Pseudopleuronectes americanus* stock enhancement effort. Aquacult. Res. 41:602–606.

Friedlander, A. M., and D. A. Ziemann.
2003. Impact of hatchery releases on the recreational fishery for Pacific threadfin (*Polydactylus sexfilis*) in Hawaii. Fish. Bull. 101:32–43.

Gregorakis, K., M. N. Alexis, K. D. A. Taylor, and M. Hole.
2002. Comparison of wild and cultured gilthead sea bream (*Sparus aurata*); composition, appearance and seasonal variations. Int. J. Food Sci. Technol. 37:477–484.

Haight, W. R., D. R. Kobayashi, and K. E. Kawamoto.
1993a. Biology and management of deepwater snappers of the Hawaiian Archipelago. Mar. Fish. Rev. 55(2):17–24.

Haight, W. R., J. D. Parrish, and T. A. Hayes.
1993b. Feeding ecology of deepwater lutjanid snappers at Penguin Bank, Hawaii. Trans. Am. Fish. Soc. 122:328–347.

Handeland, S. O., Björnsson, A. M. Arnesen, and S. O. Stefansson.
2003. Seawater adaptation and growth of post-smolt Atlantic salmon (*Salmo salar*) of wild and farmed strains. Aquaculture 220:367–384.

Leber, K. M.
1995. Significance of fish size-at-release on enhancement of striped mullet fisheries in Hawaii. J. World Aquacult. Soc. 26:143–153.

Leber, K. M., and S. M. Arce.
1996. Stock enhancement in a commercial mullet, *Mugil cephalus* L., fishery in Hawaii. Fish. Manage. Ecol. 3:261–278.

Leber, K. M., N. P. Brennan, and S. M. Arce.
1998. Recruitment patterns of cultured juvenile Pacific threadfin. *Polydactylus sexfilis* (Polynemidae), released along sandy marine shores in Hawaii. Bull. Mar. Sci. 62:389–408.

Leber, K. M., R. N. Cantrell, and P. S. Leung.
2005. Optimizing cost-effectiveness of size at release in stock enhancement programs. N. Am. J. Fish. Manage. 25:1596–1608.

Leis, J. M.
1987. Review of the life history of tropical groupers (Serranidae) and snappers (Lutjanidae). *In* Tropical snappers and groupers: biology and fisheries management (J. J. Polovina and S. Ralston, eds.), p. 189–237. Westview Press Inc., Boulder, CO.

Leis, J. M., and K. Lee.
1994. Larval development in the lutjanid subfamily Etelinae (Pisces): the genera *Aphareus*, *Aprion*, *Etelis* and *Pristipomoides*. Bull. Mar. Sci. 55:46–125.

Lino, P. G., L. Bentes, D. Abecasis, M. Neves dos Santos, and K. Erzini.
2009. Comparative behavior of wild and hatchery reared white sea bream (*Diplodus sargus*) released on artificial reefs off the Algarve (southern Portugal). *In* Tagging and tracking of marine animals with electronic devices (J. L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage, and J. Sibert, eds.), Rev: Methods Technol. Fish Biol. Fish. 9:23–34.

Manderson, J. P., L. L. Stehlik, J. Pessutti, J. Rosendale, and B. Phelan.
2014. Residence time and duration for predators in a small mid-Atlantic estuary. Fish. Bull. 112:144–158.

McCleave, J. D., and K. A. Stred.
1975. Effect of dummy telemetry transmitters on stamina of Atlantic salmon (*Salmo salar*) smolts. J. Fish. Res. Board Can. 32:559–563.

Moffitt, R. B., and F. A. Parrish.
1996. Habitat and life history of juvenile Hawaiian pink snapper, *Pristipomoides filamentosus*. Pac. Sci. 50:371–381.

Parrish, F. A.
1989. Identification of habitat of juvenile snappers in Hawaii. Fish. Bull. 87:1001–1005.

Parrish, F. A., E. E. DeMartini, and D. M. Ellis.
1997. Nursery habitat in relation to production of juvenile pink snapper, *Pristipomoides filamentosus*, in the Hawaiian Archipelago. Fish. Bull. 95:137–148.

Periago, Ma. J., Ma. D. Ayala, O. López-Albors, I. Abdel, C. Martínez, A. García-Alcázar, G. Ros, and F. Gil.
2005. Muscle cellularity and flesh quality of wild and farmed sea bass, *Dicentrarchus labrax L.* Aquaculture 249:175–188.

Schumacher, B. D.
2011. Habitat use and trophic ecology of the introduced snapper *Lutjanus kasmira* and native goatfishes in Hawaii. Ph.D. diss., 238 p. Univ. Hawaii, Honolulu, HI.

Siderius M., M. B. Porter, P. Hursky, V. McDonald, and Kauai Ex Group.
2007. Effects of ocean thermocline variability on noncoherent underwater acoustic communications. J. Acoust. Soc. Am. 121:1895–1908.

Siegel, S., and N. J. Castellan Jr.
1988. Nonparametric statistics for the behavioral sciences, 2nd ed., 399 p. McGraw-Hill, New York.

Uchida, R. N., and J. H. Uchiyama.
1996. Fishery atlas of the Northwestern Hawaiian Islands. NOAA Tech. Rep. NMFS 38, 142 p.

Weng, K. C.
2013. A pilot study of deepwater fish movement with respect to marine reserves. Anim. Biotelem. 1:17.

Yokota T., R. Masuda, N. Arai, H. Mitamura, Y. Mitsunaga, H. Takeuchi, and T. Tsuzaki.
2007. Hatchery-reared fish have less consistent behavioral pattern compared to wild individuals, exemplified by red tilefish studied using video observation and acoustic telemetry tracking. Hydrobiologia 582:109–120.

Zeller, D., M. Darcy, S. Booth, M. K. Lowe, and S. Martell.
2008. What about recreational catch? Potential impact on stock assessment for Hawaii's bottomfish fisheries. Fish. Res. 91:88–97.

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Temporal changes in abundance of harbor porpoise (*Phocoena phocoena*) inhabiting the inland waters of Southeast Alaska

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Abstract—Abundance of harbor porpoise (*Phocoena phocoena*) was estimated from data collected during vessel surveys conducted throughout the inland waters of Southeast Alaska. Line-transect methods were used during 18 seasonal surveys spanning 22 years (1991–2012). Estimates were derived from summer surveys only because of the broader spatial coverage and greater number of surveys during this season than during other seasons. Porpoise abundance varied when different periods were compared (i.e., 1991–1993, 2006–2007, and 2010–2012); however, persistent areas of high porpoise densities occurred in Glacier Bay and Icy Strait, and off the town of Wrangell and Zarembo Island. Overall abundance of harbor porpoise significantly declined from the early 1990s (N=1076, 95% confidence interval [CI]=910–1272) to the mid-2000s (N=604, 95% CI=468–780). This downward trend was followed by a significant increase in the early 2010s (N=975, 95% CI=857–1109) when abundance rose to levels similar to those observed 20 years earlier. Potential factors that could contribute to the downward trend were examined. The 2 regions with high densities of harbor porpoise (i.e., Glacier Bay and Icy Strait as well as Wrangell and Zarembo islands), that were consistently occupied by this species, and the different trend values of these 2 regions indicate that some fine-scale population structuring may exist for harbor porpoise inhabiting the inland waters of Southeast Alaska.

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Harbor porpoise (*Phocoena phocoena*) are distributed throughout Alaska waters (Fiscus et al.[1]; Leatherwood and Reeves, 1978; Leatherwood et al.[2]; Lowry et al.[3,4]; Dahlheim et al., 2000, 2009; Hobbs and Waite, 2010), commonly inhabiting waters less than 100 m deep (Barlow, 1988; Carretta et al., 2001; Hobbs and Waite, 2010). Currently, 3 stocks of harbor porpoise are recognized in Alaska: 1) the Southeast Alaska stock—occurring from Dixon Entrance (54°30′N; 134°00′W) to Cape Suckling (60°00′N; 144°00′W), 2) the Gulf of Alaska stock—occurring from Cape Suckling to Unimak Pass, and 3) the Bering Sea stock—occurring throughout the Aleutian Islands and all waters north of Unimak Pass (Allen and Angliss, 2012). The boundaries of these 3 stocks are based on geography and

[1] Fiscus, C. H., H. W. Braham, R. W. Mercer, R. D. Everitt, B. D. Krogman, P. D. McQuire, C. E. Peterson, R. M. Sonntag, and D. Withrow. 1976. Seasonal distribution and relative abundance of marine mammals in the Gulf of Alaska, 238 p. Northwest Fish. Sci. Cent. Processed Rep., [Available from Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., 7600 Sand Point Way NE., Seattle, WA 98115.]

[2] Leatherwood, S., A. E. –Bowles, and R. R. Reeves. 1983. Endangered whales of the eastern Bering Sea and Shelikof Strait, Alaska. Results of aerial surveys April 1982 through April 1983 with notes on other marine mammals seen. Hubbs Sea World Research Institute Technical Report No. 83-159, 315 p. [Available from the Natl. Mar. Mamm. Lab., Alaska Fish. Sci. Cent.,7600 Sand Point Way NE., Seattle, WA 98115.]

[3] Lowry, L. F., K. J. Frost, and J. J. Burns. 1982. Investigations of marine mammals in the coastal zone of western Alaska during summer and autumn. Annual report on contract NA 81 RAC0050, submitted to NOAA, Outer Continental Shelf Environmental Assessment Program, Juneau, Alaska, 37 p. [Available from the Natl Mar. Mamm. Lab., Alaska Fish. Sci. Cent.,7600 Sand Point Way NE., Seattle, WA 98115.]

[4] Lowry, L. F., K. J. Frost, D. G. Calkins, G. L. Swartzman, and S. Hills. 1982. Feeding habits, food requirements, and status of Bering Sea marine mammals. Vol. 1. Final report submitted to the North Pacific Fishery Management Council, Anchorage, Alaska, 292 p. [Available from the Natl. Mar. Mamm. Lab., Alaska Fish. Sci. Cent.,7600 Sand Point Way NE., Seattle, WA 98115.]

perceived areas of low porpoise density, but to date there has been no analysis of genetic or individual movement to assess the validity of these designations.

The preference of harbor porpoise for shallower waters makes them highly vulnerable to incidental capture during net-fishing operations (Jefferson and Curry, 1994; Read, 1994; Barlow et al., 1995). The nature and magnitude of incidental takes are currently unknown but could be significant in some gill-net and purse-seine fisheries targeting Alaska salmon (*Oncorhynchus* spp.) and Pacific herring (*Clupea pallasi*).

Obtaining abundance estimates for harbor porpoise, a small, inconspicuous cetacean species, is challenging. For example, the ability to detect harbor porpoise is highly sensitive to environmental conditions; surveys should be limited to relatively calm sea states and good lighting conditions. Despite such challenges, estimates of both density and abundance for this species do exist for Alaska waters. Taylor and Dawson (1984) reported on a shore-based study that yielded density estimates for Glacier Bay National Park and Preserve. In 1991–1993, and again in 1997–1999, aerial surveys of coastal waters in Alaska, ranging from the southeastern Bering Sea to Dixon Entrance, yielded more recent abundance estimates (Dahlheim et al., 2000; Hobbs and Waite, 2010).

In this study, we report the results from dedicated line-transect surveys conducted to determine the density and abundance of harbor porpoise in Southeast Alaska over a 22-year period from 1991 through 2012. The objectives of these surveys were 1) to obtain relative abundance estimates of harbor porpoise within the inland waterways of Southeast Alaska, 2) to investigate porpoise density and abundance by different strata (i.e., smaller regions), 3) to establish a baseline for detecting changes in harbor porpoise abundance through time, and 4) to report on significant insights on this species as a result of these investigations.

Materials and methods

Study area

The study area included the inland waters of Southeast Alaska (Fig. 1). Surveys covered all major channels or bays from Juneau to Ketchikan: Lynn Canal, Icy Strait, Glacier Bay, Cross Sound, Chatham Strait, Stephens Passage, Frederick Sound, Sumner Strait, and Clarence Strait. When time permitted or weather precluded the surveying of major channels, many adjacent smaller bodies of water (bays, inlets, and passages) were surveyed. The coverage of these smaller areas varied considerably among surveys and across the years.

Field methods (1991–1993)

During 1991–1993, surveys were carried out aboard the NOAA Ship *John N. Cobb*, a 28.4 m long research vessel with a combined bridge and average observer height of 5.9 m. A line-transect method was employed to survey predetermined tracklines. At the start of this study, distribution, habitat preferences, and seasonal occurrence of harbor porpoise within the study area were unknown. Tracklines were designed throughout the study area with either a zig-zag or straight-line path, depending upon the size of the different areas. The survey was designed to include all major waterways and a selection of smaller bays and inlets to examine both deepwater and nearshore habitats throughout the entire study area. The same trackline design was employed for all surveys completed between 1991 and 1993, although alterations were made during some surveys depending on weather and other unforeseen circumstances (e.g., mechanical breakdowns or engagement in rescue operations).

During line-transect surveys, sighting data were collected by a team of 3 observers, with 1 observer at each of 3 stations: starboard, port, and recorder station. In the early 1990s, the total number of biologists participating in the survey was 6; therefore, a full observer rotation took 2 h, with each observer spending 40 min at each station or watch, followed by a 2-h rest period for each observer after each full rotation of watches. Schedules for observer rotations were selected randomly each day.

Port and starboard observers used 7×50 Fujinon[5] binoculars (model 56A2, Fujifilm Holdings Corp., Tokyo) to search from 0° (at the ship's bow) to 90°. Scanning techniques were standardized with nearly 32 min (or 80%) of the 40-min watch spent scanning with the binoculars and about 8 min spent scanning with the naked eye. To reduce observer fatigue, binoculars were supported by adjustable metal poles that were either handheld or rested on the observer's hips. When not entering data, the recorder searched for porpoise by scanning both sides of the ship from the bridge with the naked eye. Binoculars were only used by the recorder to confirm sighting identifications and numbers. Sightings made by the officers, crew, and off-watch observers were recorded as "off effort" and were not used in calculations of density estimates.

A GPS unit was connected directly to a portable computer on the bridge. The date, time, and position of the ship were automatically entered into a data file every 10 min and whenever data were entered by the recorder. Search effort was recorded on the computer by marking the beginning and end of each transect. Beaufort sea state, a weather description (rain and fog), a visibility index, and observer positions (port, recorder, and starboard) were also entered. A new entry was made whenever a change in course, weather, or personnel occurred.

When a sighting was made, the recorder entered the following data: all sightings made by the port and starboard observers, the sighting angle, number

[5] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Figure 1

Map of study area in Southeast Alaska, with regions (strata), identified by numbers, where line-transect surveys of harbor porpoise (*Phocoena phocoena*) were conducted from vessels in inland waters over the periods1991–1993, 2006–2007, and 2010–2012.

of reticles to the sighting, radar distance (in nautical miles) to the shoreline at the same angle of the sighting, the species sighted, the number of individuals seen (best, high, and low counts), and the direction of travel of the animal(s). The sighting angle was obtained from peloruses mounted on the port and starboard bridge. To obtain distance to a sighting, Fujinon binoculars equipped with internal reticles were used. The top reticle was placed on the horizon or shoreline, and the number of reticles down to the location of the sighting was counted to the nearest tenth of a reticle. The reticle binoculars were calibrated with the ship's radar to objects of known distances.

Field methods (2006, 2007, and 2010–2012)

When line-transect surveys resumed in 2006 and 2007 aboard the *John N. Cobb,* it was recognized that there was considerable patchiness in the distribution and variation in density of harbor porpoise throughout the inland waters of Southeast Alaska, such that assigning a single density estimate to the whole study area was not appropriate. Consequently, smaller regions (strata) were established that were characterized by different geographic features: bays; inlets; deepwater channels, such as Icy Strait and Chatham Strait; and large areas of exposed waters, such as Frederick Sound. Allocation of stratum-specific effort by region was based on harbor

porpoise densities derived from the results of the surveys conducted in 1991–1993. Regions with higher porpoise density in the early 1990s than other regions within the same period were given greater trackline effort in the later surveys. As in the early years, both zig-zag and straight-line paths were used for tracklines in an effort to include as many different habitats as possible.

Between 2010 and 2012, the following 4 charter vessels were used to conduct our surveys: July 2010, the FV *Steller* (21.3-m commercial fishing vessel with a combined bridge and observer height of 4.8 m); September 2010, the FV *Northwest Explorer* (43.8-m research and fishing vessel with a combined bridge and observer height of 5.6 m); June and September 2011, the Alaska Department of Fish and Game's RV *Medeia* (33.5-m research vessel with a combined bridge height and observer height of 7.4 m); and July 2012, the RV *Aquila* (50.0-m commercial fishing vessel with a combined bridge and observer height of 7.2 m). Different vessels were used because the *John N. Cobb* was decommissioned in 2008.

During all line-transect surveys, a team of 3 researchers (1 recorder and 2 observers) were on effort at any given time. However, the total number of biologists participating in a survey varied and determined the amount of time that observers spent off effort. The surveys conducted in 2006 and 2007 comprised 4 biologists, allowing 1 researcher to be off effort while the others manned stations. A full observer rotation took 1.5 h, during which each observer spending 30 min at each station. In this case, the observer only had a rest period of 30 min between watches. To minimize fatigue, we also went off effort for meals, a schedule that provided each observer with an additional rest period. In 2010, 5 biologists participated in the survey. As with the 2006 and 2007 surveys, a full observer rotation took 1.5 h with a 1-h rest period between watches. In 2011 and 2012, a full complement of 6 biologists participated in the surveys, allowing observers to spend 30 min at each station and have a 90-min rest period. As noted earlier for the surveys conducted during 1991–1993, schedules of observer rotations were selected randomly each day.

To gather positional and navigational information, the computer used for data collection was either interfaced directly to the ship's GPS system (2006 and 2007) or connected to a portable GPS unit (2010–2012). The computer program WinCruz (R. Holland, NOAA Southwest Fisheries Science Center) was used to record all sighting and environmental data (e.g., cloud cover, wind strength and direction, and sea conditions). All other field methods for data collection (e.g., scanning techniques and field equipment) were the same as those used for surveys conducted in the early 1990s.

Analysis for corrected distances

For the surveys conducted during 2006–2012, distance from the vessel to the animal was originally recorded in WinCruz under the inherent assumption that the reticle given by the observer was taken from the horizon. However, within the inland waterways of Southeast Alaska, many of the sightings occurred against the land versus the true horizon. In these instances, the observer used the shoreline as their "horizon," and the distance to the sighting needed to be recalculated.

Sightings were recorded in WinCruz as the position of the observer (vessel) at the time of a sighting. All sightings were plotted in ArcMap, vers. 10.1 (Esri, Redlands, CA), and a line representing the distance to the real horizon, at the correct sighting angle, was drawn. The horizon line was truncated wherever it crossed land. The length of this new line, representing the distance from the observer to the shore at the angle of the sighting, was then converted to "reticles to land" with the DistRet function in Geofunc (National Marine Mammal Laboratory, http://www.afsc.noaa.gov/nmml/software/excelgeo.php, accessed January 2013), a Microsoft Excel add-in that performs trigonometric calculations for plane and spherical geometry pertinent to marine mammal survey sighting methods (the appropriate formulas are described in Lerczak and Hobbs [1998]), to account for the corresponding observer height and radians per reticle for 7×50 binoculars. The resulting value of reticles to land was added to the original observer reticles to calculate the actual reticles of the animal from the vessel. Final distance from the observer to the animal was calculated from this new reticle value with the DistRet function. During the 1991–1993 surveys, observers obtained a distance to shore at the angle of the sighting from the ship's radar; however, to be consistent with distances calculated for sightings in the later surveys, the above protocol also was applied for all harbor porpoise sightings for those years.

Line-transect estimation of density and abundance

The density and abundance of harbor porpoise was estimated for 3 survey periods, 1991–1993, 2006–2007, and 2010–2012, and effort was allocated in 6 strata that were defined on the basis of distribution of harbor porpoise throughout Southeast Alaska and the configuration of different water features (such as large straits and bays). Data were pooled across sequential years as a strategy to minimize variability due to the spatial distribution of harbor porpoise and the allocation of survey effort, therefore, providing more robust estimates of abundance for the 3 different periods.

Previous studies reported no evidence of seasonal changes in distribution for harbor porpoise occupying the inland waters of Southeast Alaska (Dahlheim et al., 2009). Therefore, given the broader spatial coverage and greater number of surveys conducted in summer, we chose to derive abundance estimates from the summer season only.

Estimation of detection probability

Often, when the collection of sighting data is consistent across years or strata in visual line-transect sur-

Table 1

Details about the 18 line-transect surveys for harbor porpoise (*Phocoena phocoena*) conducted from vessels in the inland waters of Southeast Alaska in 1991–2012 during spring, summer, and fall seasons.

Year	Season	Survey dates	Number of days surveyed	Vessel
1991	spring	20 April–3 May	14	NOAA Ship *John N. Cobb*
	summer	15–25 July	11	*John N. Cobb*
	fall	12–25 September	14	*John N. Cobb*
1992	spring	29 April–12 May	14	*John N. Cobb*
	summer	11–24 June	14	*John N. Cobb*
	fall	10–23 September	13	*John N. Cobb*
1993	spring	30 April–13 May	14	*John N. Cobb*
	summer	7–20 June	14	*John N. Cobb*
2006	spring	1–11 May	11	*John N. Cobb*
	summer	7–17 July	11	*John N. Cobb*
2007	spring	19–28 April	10	*John N. Cobb*
	summer	7–17 July	10	*John N. Cobb*
	fall	10–20 September	10	*John N. Cobb*
2010	summer	19 July–1 August	14	FV *Steller*
	fall	9–22 September	14	FV *NW Explorer*
2011	summer	1–14 June	14	RV *Medeia*
2011	fall	25 August–7 September	14	RV *Medeia*
2012	summer	7–20 July	14	RV *Aquila*
			Total 230	

veys, perpendicular distance data are pooled to obtain a single detection function for the whole study period and area, and that pooled detection function is then used to compute annual or stratum-specific abundance estimates (e.g., Hammond et al., 2002; Barlow, 2006; Zerbini et al., 2006). In the present analysis, to minimize variability between survey periods that could lead to biased estimates of this parameter because of the temporal changes in survey protocols described above, detection probabilities (P) were estimated for each period by pooling perpendicular distances for the periods 1991–1993, 2006–2007, and 2010–2012 separately. Detection probability was estimated by modeling ungrouped data of perpendicular distances that were truncated at 2 km by using both conventional distance sampling (CDS) and multiple covariate distance sampling (MCDS) approaches (Buckland et al., 2001; Marques and Buckland, 2003). The two methods differ in that MCDS allows for the inclusion of environmental covariates in the estimation of detection probability (Innes et al., 2002; Marques and Buckland, 2003).

Models were proposed to investigate the effects of covariates on P, and the models included group size as continuous covariates with year and Beaufort category as factor covariates. The Beaufort category had 2 levels: a "low" sea state (Beaufort 0–2) and a "high" sea state (Beaufort >3). In addition, a "ship" covariate was proposed for the period 2010–2012 to assess whether the use of ships with different height platforms had an effect on detection probability. This covariate had 4 levels, namely 1 level for each ship used during the summer surveys.

For each year, covariates were tested singly or in additive combination. It was expected that P was positively correlated with group size and platform height but negatively correlated with Beaufort sea state. If a proposed model was inconsistent with these expectations, then that model was deleted from the analysis before model selection was performed (e.g., Zerbini et al., 2006). The model with the lowest Akaike's information criterion (AIC) was used for statistical inference (Burnham and Anderson, 2002). In the estimates provided here, the probability of detecting porpoise on the trackline was assumed to be unity ($g(0)=1$; see *Discussion* section).

Estimation of group size

Porpoise were considered to be in a group when animals were within 10–15 body lengths of each other. Group size has the potential to affect estimates of P. If larger groups are easier to detect further away from the trackline, then use of average group size can bias estimates (Buckland et al., 2001). In our exploratory analysis, regression of group size versus detection probability (Buckland et al., 2001) indicated that detections were independent of group size. Therefore, stratum-specific simple means were used after trunca-

Table 2

Regions identified within the study area with overall size of each stratum and the amount of survey effort realized during line-transect surveys for harbor porpoise (*Phocoena phocoena*) conducted in summer in Southeast Alaska in 3 survey periods (1991–1993, 2006–2007, and 2010–2012).

			Survey effort (km)		
Region	Region name	Area (km^2)	1991–1993	2006–2007	2010–2012
1	Cross Sound, Icy Strait, and Glacier Bay	2302	1210	522	1122
2	Lynn Canal and Stephens Passage	1985	740	345	526
3	Frederick Sound	2951	1059	579	1279
4	Upper and Lower Chatham Strait	4267	957	354	694
5	Sumner Strait, Wrangell, and Zarembo Island	2943	812	450	1136
6	Clarence Strait to Ketchikan	3218	533	159	599
Total		17,665	6228	2466	6172

tion to estimate the expected group size for analysis conducted with CDS models. For MCDS models, estimates of the expected group size were obtained as proposed by Marques and Buckland (2003, Eq. 16 on p. 928).

Estimation of abundance

Stratum-specific abundance was estimated with the most supported detection probability model for each period. Total abundance in the survey regions was estimated by summing across the estimates of each individual stratum. Abundance and variance were estimated as in Innes et al. (2002) and Marques and Buckland (2003). Lognormal 95% confidence intervals (CIs) (Buckland et al., 2001) were computed for abundance estimates for each period.

Results

Between 1991 and 2012, 8 line-transect surveys were completed during the summer in Southeast Alaska (Table 1). The regions (or strata) within the study area are depicted in Figure 1. Total and stratum-specific regions and realized survey effort are summarized in Table 2. In all regions combined, a total area of 17,665 km^2 representing 14,865 km of survey trackline was surveyed.

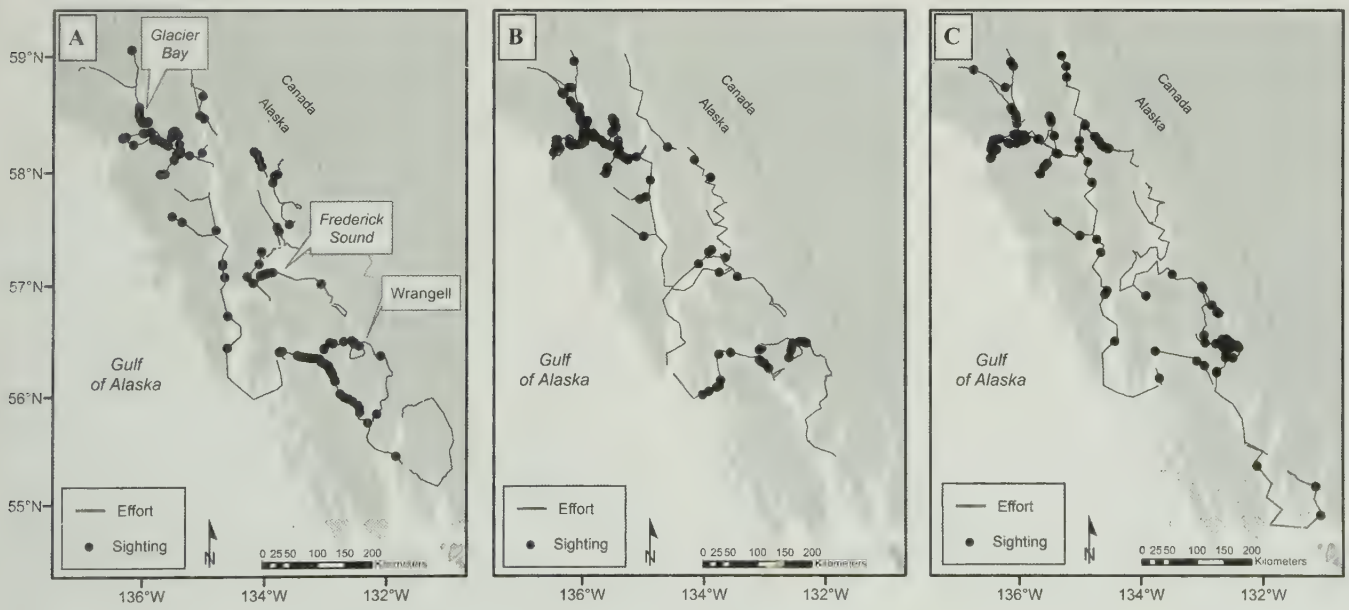

Figure 2

Sightings of harbor porpoise (*Phocoena phocoena*) and completed tracklines for line-transect surveys conducted in the inland waters of Southeast Alaska during summer in (**A**) 1991, (**B**) 1992, and (**C**) 1993.

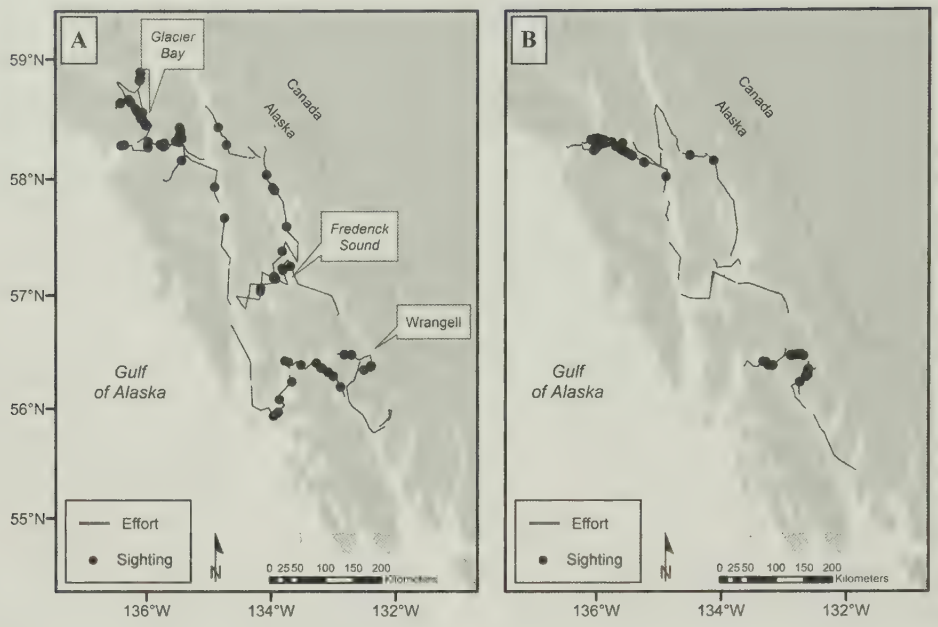

Figure 3

Sightings of harbor porpoise (*Phocoena phocoena*) and completed tracklines for line-transect surveys conducted in the inland waters of Southeast Alaska during summer in (**A**) 2006 and (**B**) 2007.

Completed tracklines and harbor porpoise sightings are depicted for each of the 3 periods in Figures 2–4.

Estimation of detection probability

Parameter estimates for the models most supported by AIC for each period are presented in Table 3, and their equivalent detection functions are illustrated in Figure 5. Estimation of P varied between 0.47 (coefficient of variation [CV]=0.04) and 0.61 (CV=0.04). The half-normal model with a Beaufort category covariate was selected as the best fit for the periods 1991–1993 and 2010–2012, and the hazard rate model without covariates was the most supported model in 2006–2007.

Encounter rates and estimation of group size

Sightings and group encounter rates are presented in Table 4. The total number of harbor porpoise groups seen in inland waters in Southeast Alaska during the summer was 422, 137, and 434 for the periods 1991–1993, 2006–2007, and 2010–2012, respectively. However, because of truncation of perpendicular distance data, the number of sightings used in the estimation of density was 381, 130, and 412 for each period. The greatest average encounter rate was observed in the period 2010–2012 (0.07 groups/km, CV=0.17) and the lowest was recorded within the period 2006–2007 (0.05 groups/km, CV=0.20). Expected average group sizes (Table 5) ranged from 1.37 (CV=0.03, during 2010–2012) to 1.59 individuals/group (CV=0.05, during 1991–1993).

Estimation of density and abundance

Stratum-specific estimates of density and abundance of harbor porpoise in Southeast Alaska during the summer are summarized in Table 6. Overall, density was similarly high in the earliest (1991–1993, density (D)=0.06, CV=0.13) and the latest (2010–2012, D=0.06, CV=0.10) periods. In contrast, density declined by half during the period 2006–2007 (D=0.03, CV=0.20). Overall estimates of abundance indicated a significant decline in the numbers of Southeast Alaska harbor porpoise from the levels observed in the early 1990s (N=1076, 95% CI=910–1272) to the mid-2000s (N=604, 95% CI=468–780) a drop that was followed by a significant increase in the early 2010s (N=975, 95% CI=857–1109) when the population reached numbers similar to those observed 20 years earlier (Table 6, Fig. 6).

Regions of higher density were consistently found near Glacier Bay and Icy Strait (region 1; the northern region of the study area) and around Zarembo Island and the town of Wrangell (region 5; the southern region of the study area), with mean densities in these 2 regions nearly 2 and 4 times greater, respectively, than the mean overall density of harbor porpoise in Southeast Alaska. Abundance in these 2 regions corresponded to 75–88% of the overall harbor porpoise abundance in the study area (Table 6), but trends in abundance differed between them. Although region 5, with Zarembo Island and Wrangell, showed a pattern similar to the one seen in the whole of Southeast Alaska, that is to say, they showed a significant decline from the early 1990s to the mid-2000s followed by a significant in-

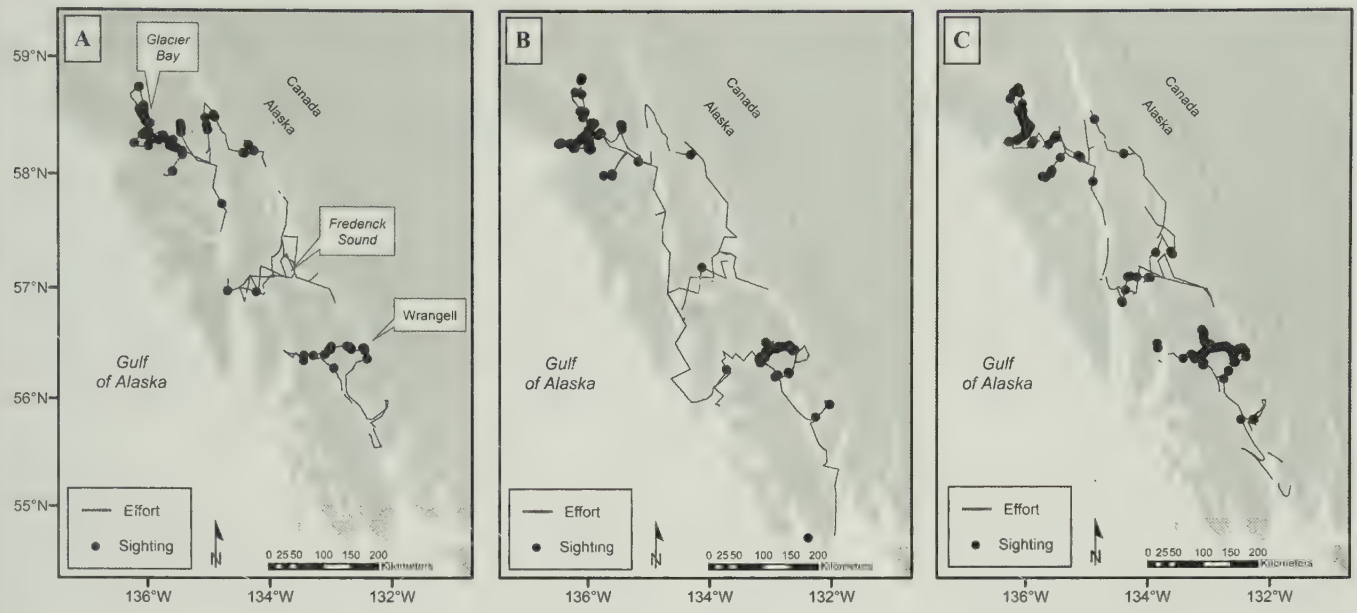

Figure 4

Maps with locations of sightings of harbor porpoise (*Phocoena phocoena*) and completed tracklines for line-transect surveys conducted in the inland waters of Southeast Alaska during summer in (**A**) 2010, (**B**) 2011, and (**C**) 2012.

crease in the early 2010s, abundance in region 1, with Glacier Bay and Icy Strait, remained relatively stable during the 22-year period of this study (Table 6, Fig. 6).

Discussion

Estimation of abundance

Overall abundance was found to vary among survey periods in this 22-year study (1991–2012). The abundance (N=1076) in the early 1990s in the first survey period was relatively high, lower for the period 2006–2007 (N=604) and higher again for the period 2010–2012 (N=975). Because the surveys conducted in this study covered a long period of time, they were subject to some changes in methods that could affect the abundance estimates. In addition, multiple factors could have affected the sightability and identification of harbor porpoise groups, and these factors are discussed below.

To the best of our ability, we kept survey effort comparable throughout the years. With the exception of the 2007 survey, during which effort was reduced because of a 3-day mechanical breakdown and fog conditions encountered throughout various regions of the survey area, effort remained fairly consistent and only minor changes were made in trackline and coverage because of adverse weather conditions, ship mechanical breakdowns, or cruise duration. However, the number of biologists who participated in the survey varied over the 22-year study period from 4 to 6 due to either the lack of vessel accommodations or NOAA restrictions. Both experienced and inexperienced observers were used and some individuals participated in several different surveys and one observer participated in all surveys.

Table 3

Most supported models of detection probability and estimates of detection probability of harbor porpoise (*Phocoena phocoena*) in Southeast Alaska during the periods 1991–1993, 2006–2007, and 2010–2012. hn=half normal; hr=hazard rate; Beaufort=Beaufort sea state; CV=coefficient of variation; P=detection probability.

Year	Detection probability model	P	CV (P)
1991–1993	hn + Beaufort	0.51	0.04
2006–2007	hr	0.61	0.08
2010–2012	hn + Beaufort	0.47	0.04

Laake et al. (1997) showed that observer experience affects their ability to detect harbor porpoise in aerial surveys; inexperienced observers miss porpoise groups 2–3 times more than experienced observers. We assumed when comparing experienced with experienced observers that the same pattern would occur during vessel surveys. However, inexperienced observers can also have difficulty both with correctly estimating group size and with accurately identifying a species (NMML, unpubl. data[6]). Average group sizes did not

[6] NMML (National Marine Mammal Laboratory). 2010. Unpubl. data. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA.98115-6349.

Table 4

Sightings (*N*) of harbor porpoise (*Phocoena phocoena*) and group encounter rates (ER; groups/km) during surveys conducted in summer in Southeast Alaska inland waters during the periods 1991–1993, 2006–2007, and 2010–2012. CV=coefficient of variation.

		1991–1993			2006–2007			2010–2012		
Region	Region name	N	ER	CV	N	ER	CV	N	ER	CV
1	Cross Sound, Icy Strait, and Glacier Bay	177	0.15	0.12	71	0.14	0.29	160	0.14	0.13
2	Lynn Canal and Stephens Passage	22	0.03	0.25	7	0.02	0.39	12	0.02	0.42
3	Frederick Sound	25	0.02	0.28	10	0.02	0.38	11	0.01	0.51
4	Upper and Lower Chatham Strait	16	0.02	0.29	3	0.01	0.51	4	0.01	0.00
5	Sumner Strait, Wrangell and Zarembo Island	132	0.16	0.25	39	0.09	0.28	214	0.19	0.14
6	Clarence Strait to Ketchikan	9	0.02	0.42	–	–	–	5	0.01	0.51
Total		381	0.06	0.12	130	0.05	0.20	412	0.07	0.17

differ over the years, indicating that observer experience was not an issue.

Although experienced observers can readily discern the profile differences between a surfacing harbor porpoise and a slow rolling Dall's porpoise (*Phocoenoides dalli*), accurate species identification can prove difficult for an inexperienced observer. Occasionally, a vertical spray of water, termed a "pop splash," occurs as the porpoise breaks the water surface to breathe (Taylor and Dawson, 1984). This vertical spray of water generated by a fast-moving harbor porpoise can, at times, be confused with the characteristic spray associated with a rooster-tailing Dall's porpoise. Within the 2 major regions where harbor porpoise concentrated, Dall's porpoise sightings were either rare or very limited in numbers (Dahlheim et al., 2009). The percentage of unidentified porpoise varied across survey years from 0% to 16% of the total number of porpoise seen. Of particular interest is that the percentages of unidentified porpoise were lowest (0–3%) during the mid-2000s, when the steepest abundance declines were noted.

The experience level of observers varied during this multiyear study. However, on the basis of low variation in group size, low overlap of harbor and Dall's porpoise distribution, and the rate of unidentified porpoise sightings over the study period, the potential biases that result from observer variability are not a significant factor in the abundance estimates.

Harbor porpoise are small, have no visible blow, and have a very low profile in the water. These features are well-known constraints in visual detection of this species (e.g., Hammond et al., 2002). Sighting cues can be very subtle, and observers can easily miss sighting an animal even in the best of conditions. The majority of the surveys in our study were conducted in Beaufort sea states between 0 and 3 and that condition is reflected in the sighting data. Under these relatively good conditions, 99% of the sightings were collected. Nonetheless, models with a Beaufort category were selected in 2 out of the 3 periods, indicating that higher sea states significantly reduced the sightability of porpoise.

Over the 22-year period, 5 different vessels were used, but ship height did not influence detection of

Table 5

Average expected group size, E(S), for harbor porpoise (*Phocoena phocoena*) during surveys conducted in inland waters of Southeast Alaska during the summer season of the periods 1991–1993, 2006–2007, and 2010–2012. CV=coefficient of variation

		1991–1993		2006–2007		2010–2012	
Region	Region name	E(S)	CV	E(S)	CV	E(S)	CV
1	Cross Sound, Icy Strait, and Glacier Bay	1.6	0.06	1.73	0.06	1.41	0.06
2	Lynn Canal and Stephens Passage	1.49	0.10	1.57	0.17	1.24	0.07
3	Frederick Sound	1.74	0.10	2.30	0.19	1.73	0.14
4	Upper and Lower Chatham Strait	1.39	0.08	1.33	0.21	1.50	0.00
5	Sumner Strait, Wrangell, and Zarembo Island	1.53	0.04	1.31	0.05	1.36	0.03
6	Clarence Strait to Ketchikan	1.61	0.16	0.00	0.00	1.00	0.00
Total		1.56	0.03	1.59	0.05	1.37	0.03

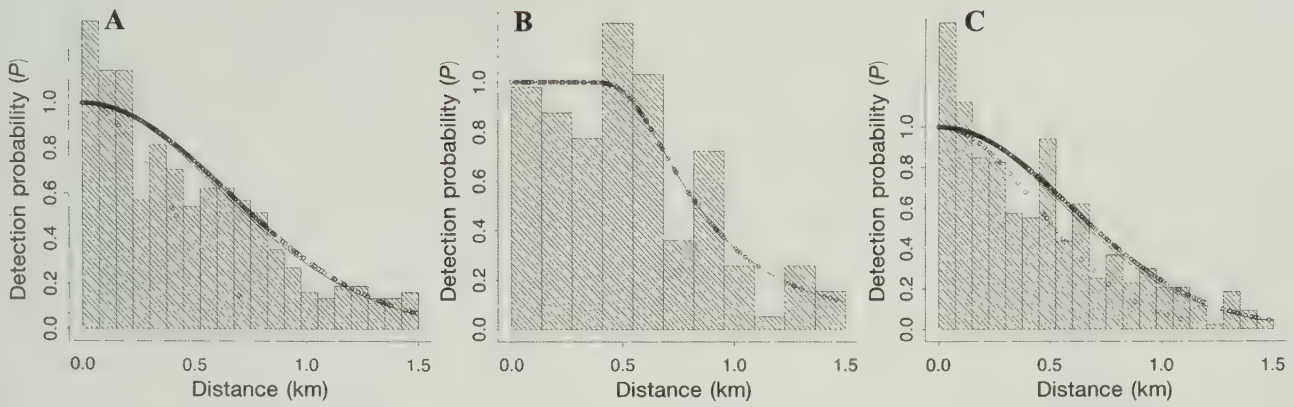

Figure 5

Detection probability models that fit perpendicular distance data collected during surveys of harbor porpoise (*Phocoena phocoena*) in Southeast Alaska for the following periods and models: (**A**) 1991–1993, half normal (hn)+Beaufort sea state; (**B**) 2006–2007, hazard rate; and (**C**) 2010–2012, hn+Beaufort sea state.

harbor porpoise, possibly because most groups were observed well within the maximum detection range provided by each ship. Animal responses may have varied on the basis of the noise profiles transmitted by these different platforms. If animals move toward or away from the survey platform during line-transect surveys, density estimates will be over- or underestimated, respectively. Palka and Hammond (2001) reported that North Atlantic harbor porpoise avoided the survey platform. However, Williams and Thomas (2007) reported that responsive movement toward or away from survey platforms was not pronounced for harbor porpoise that occupied the coastal waters of British Columbia. During our investigations, we did not observe harbor porpoise responding to our survey platform; however, quantitative data that addressed porpoise avoidance or attraction were not collected.

It is unlikely that we missed areas with high densities of harbor porpoise given the extent of our spatial coverage and the long-term nature of our study. In addition to the 8 summer surveys reported here (in 1991–1993, 2006–2007, 2010–2012), we also conducted 5 line-transect surveys each in the spring and fall (Table 1). Some areas typically not covered during our line-transect surveys (e.g., when we were off effort while entering bays and inlets to anchor for the night, finding shelter from storms, or conducting studies on killer whales; see Dahlheim and White, 2010) did not reveal any other regions of high porpoise densities. In addition, between 1994 and 2005, 24 more vessel surveys, during which line-transect methods were not carried out throughout this study area, found no other areas of high porpoise densities (Dahlheim et al., 2009). An aerial study conducted in 1997 (Hobbs and Waite, 2010) included some additional survey areas in Southeast Alaska but also did not reveal any other locations with high densities of harbor porpoise. Interviews with other researchers, local residents, and fishermen famil-

Table 6

Summer density (D; individuals/km^2) and abundance (N; number of individuals) of harbor porpoise (*Phocoena phocoena*) from surveys conducted in the inland waters of Southeast Alaska during the periods 1991–1993, 2006–2007, and 2010–2012. CV=coefficient of variation.

		1991–1993			2006–2007			2010–2012		
Region	Region name	D	N	CV	D	N	CV	D	N	CV
1	Cross Sound, Icy Strait, and Glacier Bay	0.15	342	0.14	0.13	297	0.31	0.14	332	0.14
2	Lynn Canal and Stephens Passage	0.03	65	0.24	0.02	35	0.44	0.02	40	0.42
3	Frederick Sound	0.03	81	0.32	0.02	64	0.41	0.01	30	0.54
4	Upper and Lower Chatham Strait	0.02	68	0.31	0.01	26	0.56	0.01	25	0.04
5	Sumner Strait, Wrangell, and Zarembo Island	0.16	461	0.25	0.06	182	0.29	0.18	526	0.15
6	Clarence Strait to Ketchikan	0.02	60	0.45	0.00	0	0.00	0.01	21	0.49
Total		0.06	1076	0.13	0.03	604	0.20	0.06	975	0.10

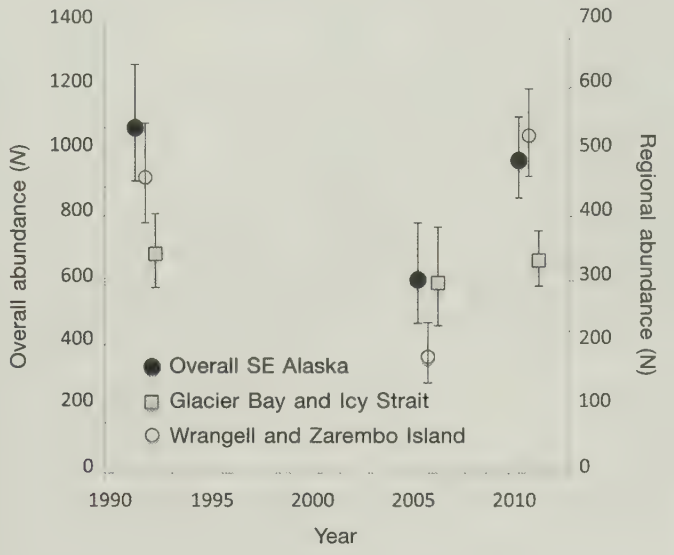

Figure 6

Estimates for overall and regional abundance of harbor porpoise (*Phocoena phocoena*) from surveys conducted in Southeast Alaska during the periods 1991–1993, 2006–2007, and 2010–2012. Note the significant declines (nonoverlapping confidence intervals) in the estimates provided for overall Southeast Alaska and for the region that included Wrangell and Zarembo Island in the mid-2000s and the relatively stable trend over the 22-year study period (1991–2012) for the region that included Glacier Bay and Icy Strait. Error bars indicate 95% confidence intervals.

iar with these waters also revealed no other areas of major porpoise concentrations.

Because of the patterns of clumped distribution observed for harbor porpoise, if we did miss an entire region where animals were concentrated both temporally and spatially, that omission would significantly affect our abundance estimate for that particular year. However, by pooling data across sequential years, we reduced the variance resulting from the naturally patchy distribution of harbor porpoise.

The abundance estimates we derived for harbor porpoise in Southeast Alaska are likely biased low for 2 major reasons. We did not sample all areas used by harbor porpoise in inlands waters of Southeast Alaska. This region encompasses an area of 27,808 km^2, but only 17,665 km^2 were actually surveyed. Although there is limited evidence that any of the regions that were not surveyed corresponded with high-density porpoise habitats, the occurrence of a small number of animals in these regions would lead to an underestimated abundance. Another important source of negative bias in results of harbor porpoise studies comes from animals that are missed along the trackline, that is from the violation of the assumption of $g(0)=1$. Previous studies have documented the importance of obtaining an estimation of the proportion of animals missed along the trackline (i.e., the proportion derived from $g[0]$ experiments) to compute absolute estimates of abundance (Barlow, 1988; Palka, 1995, 1996). These studies have shown that approximately 20–50% of harbor porpoise groups are missed.

If $g(0)$ correction factors obtained from other vessel studies (Barlow, 1988; Palka, 1995) are used to adjust for animals missed by observers, the total number of harbor porpoise in Southeast Alaska may be 1.5–2.0 times greater than the numbers reported here. However, the actual value of the correction factor for our study is unknown and may vary considerably on the basis of many aspects and circumstances that affect porpoise sightability, including visual search protocols of observers, weather and visibility conditions, survey platform, behavior of porpoise, and density of animals in different regions (Laake and Borchers, 2004; Laake et al., 1997; Palka, 1995). Clearly, $g(0)$ experiments are needed to obtain absolute abundance of harbor porpoise in Southeast Alaska. Ideally, these estimates should be survey-specific in order to assess whether and how very different survey teams and conditions affect the estimation of animals missed along the tracklines.

Before the surveys conducted in 2011 and 2012, a trend analysis, completed to include the 1991–1993, 2006–2007, and 2010 surveys, indicated a high probability of a decline in porpoise numbers ranging from 2% to 4% per year for the whole study area (Zerbini et al.[7]). However, when data from 2011 and 2012 were added to this analysis, the rate of decline over the entire study period decreased substantially and was no longer significant. The increase in abundance observed for the waters surrounding Wrangell and Zarembo Island represented a three-fold increase that is not biologically plausible given the rate at which this species reproduces. Therefore, it is likely that this increase reflected a combination of factors, including possible population growth, a shift in distribution, or the influx of porpoise from other regions (e.g., offshore waters).

It is unclear why the decline in porpoise numbers occurred between the early 1990s and the mid-2000s (Fig. 6) or, in fact, if this decline is real. The low abundance in 2006 and 2007 cannot be explained by reduced survey effort (i.e., 2 survey years versus 3 survey years for the periods 1991–1993 and 2010–2012) because similar effort per unit of area took place where high-densities of porpoise occur for all years. Given the clumped distribution of harbor porpoise in the study area, it

[7] Zerbini, A., M. E. Dahlheim, J. Waite, A. Kennedy, P. R. Wade, and P. J. Clapham. 2011. Evaluation of population declines of harbor porpoise (*Phocoena phocoena*) in Southeast Alaska inland waters. *In* Book of abstracts: 19th biennial conference on the biology of marine mammals; Tampa, FL., 28 November–2 December. Society for Marine Mammalogy, Moss Landing, CA.

is possible but unlikely, given the multiple years involved and the overall extent of the area coverage in our study, that a large grouping of animals was missed during a survey period. One explanation is that part of the population may have moved outside our study area (e.g., offshore waters) because of shifts in prey availability and abundance. Without knowing whether porpoise shift their distribution or what might drive it if they do (e.g., prey preferences or oceanographic conditions), we cannot determine whether porpoise movement patterns are a factor in the observed downward trend. In addition, a change in porpoise numbers may also be dependent upon year-to-year variations in habitat suitability, increased predation, increased mortality from bycatch, or a combination of all these factors.

When examined on a regional scale, abundance was relatively consistent throughout the survey period in the northern region that included Glacier Bay. In contrast, a significant downward trend in abundance was estimated for the southern region that included the waters surrounding Wrangell and Zarembo Island between the early 1990s and the mid-2000s, and an increase was observed for that region as of 2010. Of particular interest is that porpoise numbers declined only in regions where salmon (*Oncorhynchus* spp.) and Pacific herring net fisheries operate. Certainly, bycatch has been shown to be a significant source of porpoise mortality in other geographic areas (Gaskin, 1984; Read and Gaskin, 1988; Woodley and Read, 1991; Read et al., 1993) and may, in fact, be responsible for the downward trend observed in our data for the mid-2000s. We are unable, however, to attribute the decline in the mid-2000s to incidental takes in the net fisheries given that interaction data are not available. Regardless of the reasons for that decline, further studies are necessary to understand the possible causes of the variability observed in our study in the abundance of harbor porpoise in inland waters off Southeast Alaska.

Insights into population structure

As currently defined (see *Introduction*), the Southeast Alaska stock of harbor porpoise occurs from Dixon Entrance to Cape Suckling, including all inland and coastal waters within this region (total area=106,087 km^2). Studies that have addressed stock structure of harbor porpoise in Alaska are either not available or based on limited sampling from a particular area (Rosel et al., 1995; Chivers et al., 2002). Outside Alaska, research has shown that harbor porpoise stock structure is of a finer scale than that of the stock structure reflected in the Alaska stock assessment report for 2011 (Allen and Angliss, 2012). Stock discreteness in the eastern North Pacific was, for example, analyzed by using mitochondrial DNA from samples collected in California, Washington, and British Columbia but from only one sample from Alaska (Rosel, 1992). Results of our initial investigation indicated little interbreeding of harbor porpoise along the western coast of North America.

Further genetic testing by Rosel et al. (1995, 1999) showed that harbor porpoise in both the eastern North Pacific and North Atlantic were not panmictic and that movement was sufficiently restricted resulting in genetic differences. Furthermore, Chivers et al. (2002), using both mitochondrial and nuclear (microsatellite) DNA, examined the intraspecific structure of harbor porpoise that inhabited the eastern North Pacific and reported similar findings. These studies revealed statistically significant genetic differentiation, indicating demographic independence of fairly small subunits within the population.

Additional evidence that harbor porpoise restrict their movements has been obtained from both contaminant research and satellite tagging studies. Investigations on the pollutant loads of harbor porpoise from California to the Canadian border (Calambokidis and Barlow, 1991) also suggest restricted movement patterns of harbor porpoise. Pollutant studies produced similar results in the North Atlantic (Westgate and Tolley, 1999). Satellite-tagging operations conducted in Puget Sound, Washington, have shown that porpoise movements were fairly localized and did not occur between Neah Bay (at the entrance of the Strait of Juan de Fuca) and the San Juan Islands; these 2 regions are separated by approximately 150 km of continuous open waterways (Hanson[8]).

During our study, harbor porpoise distribution was clumped in 2 major areas that were consistent throughout the 22-year period: the waters of Glacier Bay and Icy Strait and the waters surrounding Wrangell and Zarembo Island, including the adjacent waters of eastern Sumner Strait (northern and southern regions, respectively; also see Dahlheim et al., 2009). These regions are separated by a distance of approximately 400 km. If harbor porpoise within the inland waters of Southeast Alaska behave in the same manner as harbor porpoise elsewhere have been reported to behave (i.e., movements are locally restricted), then a low level of mixing would be expected, indicating the potential for reproductive isolation between the 2 regions. The physical character of this region (e.g., hundreds of islands and a complexity of waterways) may also limit frequent movements of harbor porpoise between the 2 regions.

The difference in abundance trends between the northern and southern regions of the study area provides additional evidence that these 2 regions, where consistent porpoise concentrations have occurred over 2 decades, represent regions of population structuring for this species within the inland waters of Southeast Alaska. Of utmost concern is that incidental takes within a small region (e.g., Wrangell and Zarembo Island) could severely affect undefined localized stocks of harbor porpoise that could easily go undetected unless stock structure is identified. On a larger scale, given the wide distribution of harbor porpoise throughout

[8] Hanson, B. 2013. Personal commun. Northwest Fish. Sci. Cent., 2725 Montlake Blvd. East, Seattle, WA 98115-2097.

Alaska waters, it is likely that several other regional and subregional populations exist within the 3 currently designated stocks.

In summary, the results of our analysis with data from surveys conducted between the years 1991 and 2010 led us to believe that numbers of harbor porpoise within the inland waters of Southeast Alaska declined significantly, highlighting a potentially important conservation issue. With the inclusion of data from surveys conducted in 2011 and 2012, our analysis indicates that if a decline occurred, then the population may be recovering. It is not clear whether the observed decline and subsequent increase in abundance represent a true decline in the population or a reflection of variable local abundance related to interannual differences in prey availability, habitat suitability, or other factors.

The overall changes in abundance of harbor porpoise observed in this study could have remained undetected were it not for the long time series of this research, clearly demonstrating both the value and need for multiyear studies on long-lived mammals, such as cetaceans. Understanding the distribution, abundance, and population trends of a given species is essential for conservation efforts to be effective. On the basis of our study, we hypothesize that harbor porpoise populations within the inland waters of Southeast Alaska contain structure. Although this structure is currently unclear, we suggest that different stocks probably exist within this region. A proper assessment of the status of the harbor porpoise stock or stocks in Southeast Alaska requires a combination of research approaches, i.e., conducting coastal and inland surveys at the same time to evaluate stock abundance, exploring correction factors for this species (e.g., $g[0]$ experiments), performing genetic studies (to fully define stock structure), and using satellite telemetry (to understand porpoise movements within or across current stock boundaries).

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Literature cited

Allen, B. M., and R. P. Angliss.
2012. Alaska marine mammal stock assessments, 2011. NOAA Tech. Memo. NMFS-AFSC-234, 288 p.

Barlow, J.
1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: I. Ship surveys. Fish. Bull. 86:417–432.
2006. Cetacean abundance in Hawaiian waters estimated from a summer/fall survey in 2002. Mar. Mamm. Sci. 22:446–464.

Barlow, J., S. L. Swartz, T. C. Eagle, and P. R. Wade.
1995. U.S. marine mammal stock assessments: guidelines for preparation, background, and a summary of the 1995 assessments. NOAA Tech. Memo. NMFS-OPR-6, 73 p.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas.
2001. Introduction to distance sampling: estimating abundance of biological populations, 432 p. Oxford Univ. Press, Oxford, UK.

Burnham, K. P., and D. R. Anderson.
2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd ed., 488 p. Springer-Verlag, New York.

Calambokidis, J. and J. Barlow.
1991. Chlorinated hydrocarbon concentrations and their use for describing population discreteness in harbor porpoises from Washington, Oregon, and California. *In* Marine mammal strandings in the United Sates: proceedings of the second marine mammal stranding workshop; Miami, 3–5 December 1987 (J. E. Reynolds III, and D. K. Odell, eds.), p. 101–110. NOAA Tech. Rep. NMFS 98.

Carretta, J. V., B. L. Taylor, and S. J. Chivers.
2001. Abundance and depth distribution of harbor porpoise (*Phocoena phocoena*) in northern California determined from a 1995 ship survey. Fish. Bull. 99:29–39.

Chivers, S. J., A. E. Dizon, P. J. Gearin, and K. M. Robertson.
2002. Small-scale population structure of eastern North Pacific harbour porpoises (*Phocoena phocoena*) indicated by molecular genetic analyses. J. Cetacean Res. Manage. 4:111–122.

Dahlheim, M. E., and P. A. White.
2010. Ecological aspects of transient killer whales Orcinus orca as predators in southeastern Alaska. Wildl. Biol. 16:308–322.

Dahlheim, M., A. York, R. Towell, J. Waite J., and J. Breiwick.
2000. Harbor porpoise (*Phocoena phocoena*) abundance in Alaska: Bristol Bay to Southeast Alaska, 1991–1993. Mar. Mamm. Sci. 16:28–45.

Dahlheim, M. E., P. A. White, and J. M. Waite.
2009. Cetaceans of Southeast Alaska: distribution and seasonal occurrence. J. Biogeogr. 36:410–426.

Gaskin, D. E.
1984. The harbor porpoise *Phocoena phocoena* (L) regional populations, status, and information on direct and indirect catches. Rep. Int. Whaling Comm. 34:569–586.

Hammond, P. S., P. Berggren, H. Benke, D. L. Borchers, A. Collet, M. P. Heide-Jørgensen, S. Heimlich, A. R. Hiby, M. F. Leopold, and N. Øien.
2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. J. Appl. Ecol. 39:361–376.

Hobbs, R. C., and J. M. Waite.
2010. Abundance of harbor porpoise (*Phocoena phocoena*) in three Alaskan regions, corrected for observer errors due to perception bias and species misidentification, and corrected for animals submerged from view. Fish. Bull. 108:251–267.

Innes, S., M. P. Heide-Jørgensen, J. L.Laake, K. L. Laidre, H. J. Cleator, P. Richard, and R. E. A. Stewart.
2002. Surveys of belugas and narwhals in the Canadian High Arctic in 1996. NAMMCO Sci. Pub. 4:169–190.

Jefferson, T. A., and B. E. Curry.
1994. A global review of porpoise (Cetacea: Phocoenidae) mortality in gillnets. Biol. Conserv. 67:167–183.

Laake, J. L., and D. L. Borchers.
2004. Methods for incomplete detection at distance zero. In Advanced distance sampling (S. T. Buckland, D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas, eds.), p. 108–189. Oxford Univ. Press, Oxford, UK.

Laake, J. L., J. Calambokidis, S. D. Osmek, and D. J. Rugh.
1997. Probability of detecting harbor porpoise from aerial surveys: estimating $g(0)$. J. Wildl. Manage. 61:63–75. [Available at http://www.jstor.org/stable/3802415.]

Leatherwood, S., and R. R. Reeves.
1978. Porpoises and dolphins. *In* Marine mammals of the eastern North Pacific and arctic waters (D. Haley, ed.), p. 97–111. Pacific Search Press, Seattle.

Lerczak, J. A., and R. C. Hobbs.
1998. Calculating sighting distances from angular readings during shipboard, aerial, and shore-based marine mammal surveys. Mar. Mamm. Sci. 14:590–598.

Marques, F. F. C., and S. T. Buckland.
2003. Incorporating covariates into standard line transect analyses. Biometrics 59:924–935. [Available at http://www.jstor.org/stable/3695332.]

Palka, D.
1995. Abundance estimate of the Gulf of Maine harbor porpoise. Spec. Issue Rep. Int. Whaling Comm. 16:27–50.
1996. Effects of Beaufort sea state on the sightability of harbor porpoises in the Gulf of Maine. Rep. Int. Whaling Comm. 46:575–582.

Palka, D. L., and P. S. Hammond.
2001. Accounting for responsive movement in line transect estimates of abundance. Can. J. Fish. Aquat. Sci. 58:777–787.

Read, A. J., and D. E. Gaskin.
1988. Incidential catch of harbor porpoises by gill nets. J. Wildl. Manage. 52:517–523. [Available at http://www.jstor.org/stable/3801603.]

Read, A. J.
1994. Interactions between cetaceans and gillnet and trap fisheries in the Northwest Atlantic. Spec. Issue Rep. Int. Whaling Comm. 15:133–147.

Read, A. J., S. D. Kraus, K. D. Bisack, and D. Palka.
1993. Harbor porpoise and gill nets in the Gulf of Maine. Conserv. Biol. 7:189–193. [Available at http://www.jstor.org/stable/2386656.]

Rosel, P. E.
1992. Genetic population structure and systematic relationships of some small cetaceans inferred from mitochondrial DNA sequence variation. Ph.D. diss., 191 p. Univ. Calif. San Diego, CA.

Rosel, P. E., A. E. Dizon, and M. G. Haygood.
1995. Variability of the mitochondrial control region in populations of the harbour porpoise, *Phocoena*, on interoceanic and regional scales. Can. J. Fish. Aquat. Sci. 52:1210–1219.

Rosel, P. E., S. C. France, J. Y. Wang, and T. D. Kocher.
1999. Genetic structure of harbour porpoise *Phocoena phocoena* populations in the northwest Atlantic based on mitochondrial and nuclear markers. Mol. Ecol. 8:S41–S54.

Taylor, B. L., and P. K. Dawson.
1984. Seasonal changes in density and behavior of harbor porpoise (*Phocoena phocoena*) affecting census methodology in Glacier Bay National Park, Alaska. Rep. Int. Whaling Comm. 34:479–483.

Westgate, A. J., and K. A. Tolley.
1999. Geographical differences in organochlorine contaminants in harbour porpoises *Phocoena phocoena* from the western North Atlantic. Mar. Ecol. Prog. Ser. 177:255–268.

Williams, R., and L. Thomas.
2007. Distribution and abundance of marine mammals in the coastal waters of British Columbia, Canada. J. Cetacean Res. Manage. 9:15–28.

Woodley, T. H., and A. J. Read.
1991. Potential rates of increase of a harbor porpoise, *Phocoena phocoena*, population subjected to incidental mortality in commercial fisheries. Can. J. Fish. Aquat. Sci. 48:2429–2435.

Zerbini, A. N., J. M. Waite, J. L. Laake, and P. R. Wade.
2006. Abundance, trends and distribution of baleen whales off Western Alaska and the central Aleutian Islands. Deep-Sea Res. I 53:1772–1790.

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Depth distribution, habitat associations, and differential growth of newly settled southern Tanner crab (*Chionoecetes bairdi*) in embayments around Kodiak Island, Alaska

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Abstract—We examined depth distribution, habitat association, and growth of newly settled southern Tanner crab (*Chionoecetes bairdi*) at 4 sites around the eastern end of Kodiak Island, Alaska, during 2010 and 2011. Settlement was from April through July, and crab density peaked during May–July, at 10 crabs/m^2 in 2010 and 2.3 crabs/m^2 in 2011. By the end of August most crabs had progressed through 3–5 molt stages (instars). An association between crabs and tubes of the ampharetid polychaete *Sabellides sibirica* was observed in 2010, but it was not seen in 2011 when both crabs and worms were less abundant. Crabs in protected embayments were larger in August than crabs at open coastal sites. Crabs at protected sites were also found in shallower water than at open coastal sites—a difference that may have exposed them to higher ambient water temperature and may have accelerated their growth. Accelerated growth may in turn result in earlier maturation. Southern Tanner crabs probably settle over a wide range of depths, but shallow embayments (depths <50 m) may play a disproportionately large role in providing recruits to the adult population, due to accelerated crab growth and survival.

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Nursery habitats for many crab and fish species are often found in waters considerably shallower than those frequented by the adult population. Three features commonly characterize shallow-water juvenile nurseries. First, water temperatures are typically higher there than in adult habitat, a difference that can facilitate rapid growth (Yamashita et al., 2001; Ryer et al., 2012). Because mortality typically decreases with prey size (Sogard, 1997), rapid growth is a principal determinant of survival to adulthood. Second, shallow water usually is characterized by lower predation rates (Linehan et al., 2001; Manderson et al., 2004; Baker and Sheaves, 2007; Ryer et al., 2010). This feature follows from Heincke's Law (sensu Cushing, 1975), which holds that the abundance of larger predatory fishes increases with depth. Lastly, shallow-water nurseries often contain structurally complex habitat, such as rooted aquatic vegetation, drift algae, bivalve shell, cobble, terrestrial litter, and polychaete tubes, which can mediate predator–prey interactions (Ryer et al., 2004; Long et al., 2011, 2013a) and, therefore, further reduce the risk of predation.

Red king crab (*Paralithodes camtschaticus*), snow crab (*Chionoecetes opilio*), and southern Tanner crab (*Chionoecetes bairdi*, hereafter "Tanner crab") stocks in the North Pacific have experienced significant declines over the last 3 decades. The reasons for stock declines are little understood but are generally attributed to overfishing or climatic changes (Orensanz et al., 1998; Woodby et al., 2005). Stocks currently are considered depressed or rebuilding, and closures have occurred throughout much of Alaska. Effective management of commercial species requires not only information on the current stock size but

also an understanding of ecological processes that contribute to the strength of upcoming year classes so that fisheries may be scaled to predicted future resource availability. For depressed stocks, recovery begins with the recruitment of one or more strong year classes. Establishment of a strong year class depends upon adequate spawning stock, transport of larvae from spawning to nursery grounds (Etherington and Eggleston, 2003), appropriate settlement substrate (Wahle and Steneck, 1991), and favorable postsettlement processes (Heck et al., 2001).

Little is known about nursery areas and preferred habitats for newly settled juveniles of these North Pacific crab species. Red king crab juveniles are strongly attracted to shallow-water, structured habitat, such as cobble, algae, and hydroids (Sundberg and Clausen[1]; McMurray et al.[2]; Loher and Armstrong, 2000), which mediates their interactions with predators and larger conspecifics (Loher and Armstrong, 2000; Stevens, 2003a; Stoner, 2009; Pirtle and Stoner, 2010, Sundberg and Clausen[1]; McMurray et al.[2]). Yet, most of this knowledge has been gained through laboratory studies or the outplanting of hatchery-reared crabs; too few juveniles are encountered in the wild to make firm conclusions. Similarly, newly settled Tanner crabs are not effectively sampled by conventional sampling gears, and there is a dearth of information on their habitat preferences and early ecology. Unlike king crabs (*Paralithodes* spp.), it is believed that Tanner crabs show an affinity for burial in unconsolidated sediment throughout their lives (Rosenkranz et al., 1998), indicating lower reliance on structured habitat during the juvenile period when crabs presumably experience high mortality.

We have conducted studies on the ecology and habitat preferences of juvenile flatfish species that use shallow-water nurseries around Kodiak Island in the Gulf of Alaska since 2002. During 2002 and 2003, we conducted beam trawl hauls in Pillar Creek Cove (hereafter Pillar) and estimated densities of age-0 Tanner crabs to be <0.05 crabs/m^2 (senior author, unpubl. data). Although not quantified in subsequent years, densities of age-0 Tanner crabs appeared to remain low. However, in 2009, we began to encounter larger numbers of age-0 Tanner crabs in beam trawl hauls and, again, began enumerating them. Beam trawl hauls conducted over a range of depths indicated that crabs were at their highest density, ~2 crabs/m^2, at depths of 15–30 m (senior author, unpubl. data). This depth range also corresponded to the depths where we documented extensive areas of habitat created by the tubes of the ampharetid polychaete *Sabellides sibirica*. This polychaete has been shown to influence the depth distribution of juvenile northern rock sole (*Lepidopsetta polyxystra*) (Ryer et al., 2013).

The densities of juvenile Tanner crabs during summer in Kodiak embayments remained high from 2009 through 2011, in the range of 2–10 crabs/m^2. Although it is too soon to conclude that populations of Tanner crabs are rebuilding in the Gulf of Alaska, the occurrence of high densities of juvenile crabs has provided an opportunity to study early life-stage ecology of a commercially important species in Alaska waters. In this study, we specifically examined 1) the depth distribution of newly settled crabs and how it changes through the summer, 2) the possible association between crabs and habitat created by polychaete worm tubes, and 3) differences in crab size and distribution between embayments with varying characteristics of sediment and physical exposure. Together, these efforts represent the first significant study aimed at understanding important facets of the habitat ecology of newly settled Tanner crabs.

Material and methods

Study sites

Field work was conducted at 4 sites in the coastal waters around the eastern end of Kodiak Island, Alaska (Fig. 1). Two of these sites, Holiday Beach (hereafter Holiday; 57°41.344′N, 152°27.958′W) and Pillar (57°49.136′N, 152°25.314′W), have been the focus of juvenile flatfish habitat studies (Hurst and Abookire, 2006: Ryer et al., 2007; Stoner et al., 2007; Ryer et al., 2013). Both sites have gently sloping, sandy bottoms just offshore from beaches that are exposed to wave action from the Gulf of Alaska. The third site, in Kalsin Bay (hereafter Kalsin; 57°36.207′N, 152°26.890′W), also is characterized by a gently sloping bottom, but it has finer sediments because of its more protected location near the head of the bay. The last site, Womens Bay (hereafter Womens; 57°42.800′N, 152°31.134′W), has a narrow entrance with a relatively shallow sill (depth ~11 m) and offshore islands, which protect the inner bay from wave action. This fourth site is also characterized by a gently sloping bottom, but sediments are finer there than at the other 3 sites being composed of silty sands and muds.

Salinity and water temperature in spring and summer were generally comparable between sites, ranging from 28–32 and 5–11°C, respectively, for all 4 sites. During 2011, temperature loggers were deployed on the bottom at each site at a depth of 15 m mean lower low water (MLLW) on 20 May and recovered on 22 August. After recovery of loggers, temperature data were downloaded, averaged by day for each site, and then analyzed with analysis of variance (ANOVA) to determine if there were differences between sites.

[1] Sundberg, K., and D. Clausen. 1977. Post-larval king crab (*Paralithodes camtschatica*) distribution and abundance in Kachemak Bay, Lower Cook Inlet, Alaska, 1976, vol. 5, 36 p. Environmental studies of Kachemk Bay and Lower Cook Inlet (L. Trasky, L. Flagg, and D. Burbank, eds.). Alaska Dep. Fish Game, Anchorage, AK.

[2] McMurray, G., A. H. Vogel, and P. A. Fishman. 1984. Distribution of larval and juvenile red king crabs (*Paralithodes camtschatica*) in Bristol Bay. OCSEAP Final Rep. 53:267–477.

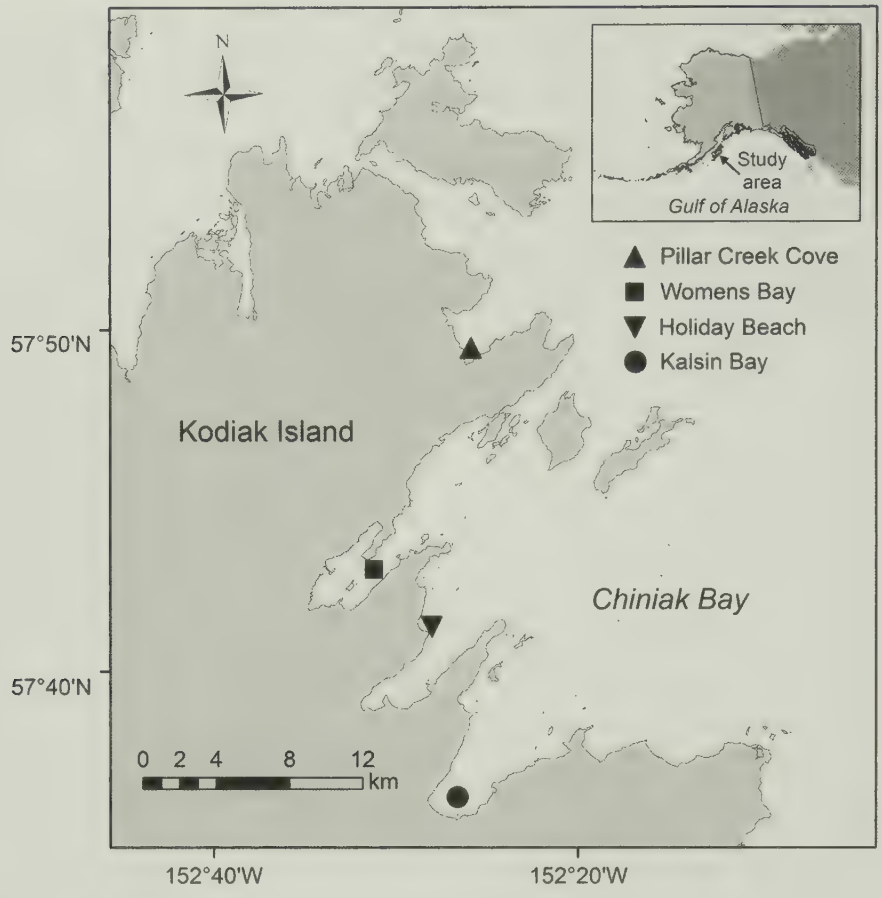

Figure 1

Map of locations of the 4 study sites around the eastern end of Kodiak Island, Alaska, where scrape tows and beam trawl hauls were conducted from May through August in 2010 and 2011 to examine the depth distribution, habitat association, and growth of newly settled southern Tanner crab (*Chionoecetes bairdi*). Inset shows location of Kodiak Island in relation to the Gulf of Alaska and Bering Sea.

Scrape estimation of crab density

Crab densities were estimated from sampling conducted with a video camera sled (Spencer et al., 2005; Stoner et al., 2007; Ryer et al., 2013). Hereafter referred to as a "scrape," the sled was augmented with a cutter bar and a codend that was 3 m long and had a 3-mm seine mesh. The tubular aluminum frame measured 114 cm long by 67 cm wide by 42 cm high. An aluminum cutter bar (width: 5 cm, thickness: 0.5 cm), mounted across the rear of the scrape between the runners and at an angle of 45°, scraped off the upper 2–3 cm of the sediment surface as the scrape was towed along the bottom of the seafloor. Fastened to the rear of the scrape and immediately behind the cutter bar, the codend had a lead line attached along its leading edge, to maintain contact with the bottom. Sediment displaced by the cutter bar passed over the lead line and into the codend. A video camera positioned just forward of the codend, at the top of the scrape, provided an oblique view of the bottom traversed. The video images were transmitted by a cable to the vessel and were recorded.

Scrape tows were made parallel to shore at depths ranging from 3 to 25 m, at a speed of 0.5 m/s for ~30 m. The actual distance towed was determined with the GPS coordinates of the start and end of each tow. On deck, the codend was briefly rinsed with seawater to remove any remaining sediment, and the contents were deposited into a plastic tray, sorted, and all Tanner crabs were enumerated. During 2010, 121 tows were made at Holiday (May: 30, June: 32, July: 29, August: 30) and 168 were completed at Pillar (May: 48, June: 47, July: 36, August: 37). In a more limited effort, we made 23 tows at Womens (July: 4, August: 19) and 4 tows at Kalsin (August: 4). During 2011, 111 tows were made at Holiday (May: 26, June: 35, July: 30, August: 20), 89 were conducted at Pillar (May: 23, June: 26, July: 20, August: 20), 132 at Womens (May: 13, June: 34, July: 42, August: 43), and 105 were completed at Kalsin (May: 25, June: 30, July: 30, August: 20). Dur-

ing each month, all tows at the 4 sites were conducted within 6 days of one another. From each scrape tow, the number of crabs per square meter was calculated on the basis of the area swept. For the purpose of analyses, scrape tows were grouped into 5-m depth bins centered on 2.5, 7.5, 12.5, 17.5, and 22.5 m.

During both 2010 and 2011, we also conducted a smaller number of tows with a 2-m plumb-staff beam trawl (hereafter referred to as a "trawl") with a 3-mm-mesh codend. This gear allowed us to sample crabs at greater depths than with the scrape, which has an operational depth limit of ~30 m. Tows were conducted at Pillar at depths of 3–80 m, parallel to shore, during July and August. We towed the trawl 200 m, and confirmed that length with GPS readings at the beginning and end of each tow. In 2010, 35 tows were completed (July: 18, August: 17), and 46 tows were made in 2011 (July: 23, August: 23). Crabs were sorted from the catch of these tows and enumerated in the laboratory. The number of crabs per square meter also was calculated on the basis of the area swept, and the resulting density values were grouped into 10-m depth bins and analyzed.

Using video from scrape tows, we characterized the relative abundance of worm tubes along each tow. During video analysis, each tow was divided into 5-s segments. For each segment, an observer assigned an index score for the relative abundance of worm tubes on the seafloor passing between the scrape's runners. The index was scored on a 5-point scale (0–4), with 0 representing worm absence and 4 representing a contiguous "worm turf" (Stoner et al., 2007; Ryer et al., 2013). The vast majority of worm tubes were easily identifiable as belonging to *S. sibirica*, following prior positive identification from benthic samples taken during 2008 (Jewett3).The tubes of *S. sibirica* are distinctive: 1.00–1.25 mm in diameter and up to 12 cm long, with approximately 70% of the tube emergent and upright above the sediment surface. For each tow, the average worm index score was calculated.

Crab density data followed a Poisson distribution. To analyze this data, we used generalized linear models (GLMs), incorporating a Poisson log-linear link function, and we used the Wald chi-square statistic for tests of significance (Wald, 1943). Crab densities were first converted to an expanded integer scale through multiplication by 10, augmentation by 1, and rounded to the nearest whole integer. We tested the resultant data for independent and interactive effects of site, month, and depth, with the worm index as a covariate. We conducted separate analyses for each year. For 2010, we excluded data for Womens and Kalsin from the analysis because of the lack of consistent temporal and depth coverage at these sites. For 2011, all 4 sites were included in analysis. Trawl data also followed a Poission distribution and were analyzed with GLM with a Poisson log-linear link, which allowed us to test for the effects of depth on crab distribution.

Diver estimation of crab density

During June, July, and August of 2010, divers used quadrats to estimate densities of crabs and worm tubes. During each dive, multiple squares made of PVC pipe were haphazardly placed on the bottom to mark the 0.25-m^2 quadrats that would be surveyed. A second square was positioned haphazardly within each of the 0.25-m^2 quadrats, marking an area of 0.10 m^2 for enumeration of worm tubes. After worm tubes were counted, the 0.10-m^2 square was removed. Then, using a metal tooth comb, a diver methodically worked over the sediment within the 0.25-m^2 quadrat, dislodging crabs and enumerating them. During the course of 10 dives, 222 paired (crab and worm tube) quadrats were sampled, with 69, 74, 59, and 20 pairs from depths of 8, 13, 17, and 23 m, respectively. Data followed a Poisson distribution and were analyzed with GLM with a Poisson log-linear link. We tested for independent and interactive effects of month and depth on crab density, with worm density included as a covariate.

Measurements of crab carapace width

We measured the carapace width of crabs from scrape tows conducted during only July and August of 2010 and during all 4 months in 2011. For tows from which more than 100 crabs were sampled, we measured a subsample of 50–100 crabs. Carapace width was measured to the nearest 0.1 mm with digital calipers. On the basis of visual examination of a cumulative size-frequency distribution, break points between peaks (instars) were identified and used to classify individuals into molt stages (C1–C5 instars). Using this classification scheme and G-tests (Sokal and Rohlf, 1969), we tested for differences in the frequency distribution of molt stages between sites for each month. In addition, we compared mean carapace width using ANOVA (Sokal and Rohlf, 1969). Where the ANOVA indicated a significant effect, group means were compared with Tukey's honestly significant difference (HSD) test (Sokal and Rohlf, 1969). Where data did not meet parametric assumptions, a Kruskal-Wallis ANOVA was used, and when significant effects were found, the associated multiple range test for differences between means was used (Conover, 1971). In these comparisons, we eliminated from consideration those crabs that were not, in our estimation, representative of the age-0 cohort (i.e., crabs of age 1 or older).

Results

Distribution of age-0 crabs

Crab densities estimated from catches of scrape tows conducted during 2010 increased from May through

[3] Jewett, S. 2008. Personal commun. Institute of Marine Science, Univ. Alaska Fairbanks, Fairbanks, AK 99775-7220.

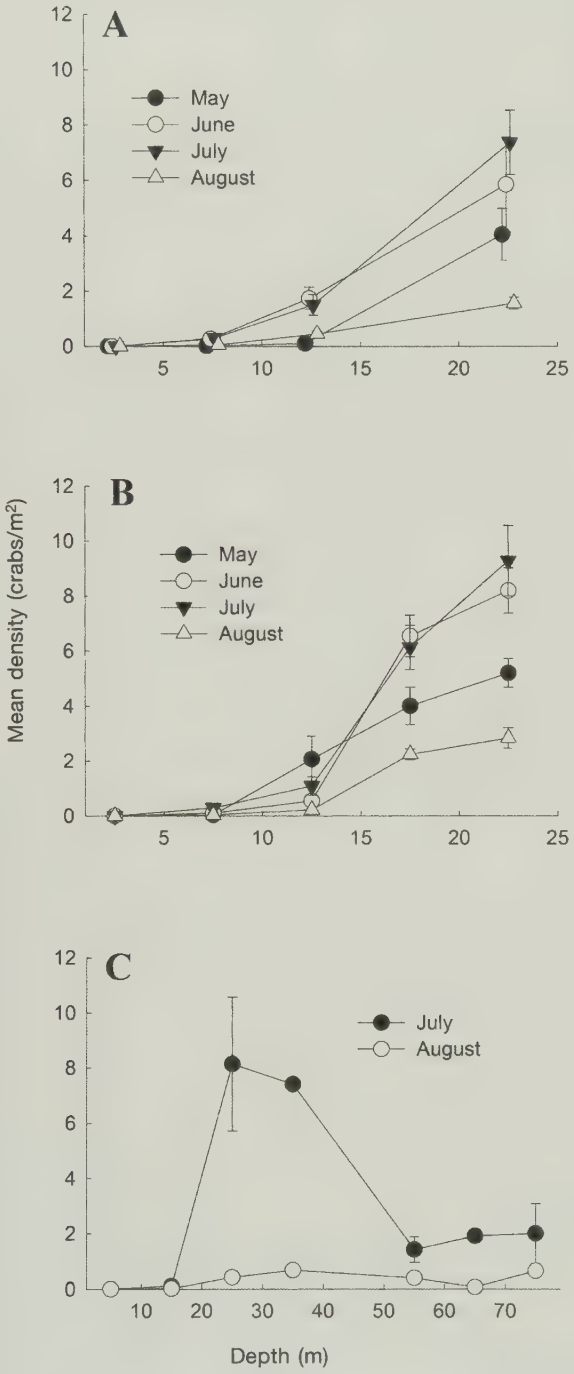

Figure 2

Mean densities of age-0 southern Tanner crabs (*Chionoecetes bairdi*), plotted against depth, from scrape tows conducted during the months of May–August in 2010 around Kodiak Island, Alaska, at (**A**) Holiday Beach and (**B**) Pillar Creek Cove and (**C**) from beam trawl hauls conducted at Pillar Creek Cove in July and August 2010. Error bars indicate standard error of the mean. Note that the depth range for beam trawl hauls on the *x*-axis in panel C is different from the range in the panels that show depths of scrape tows.

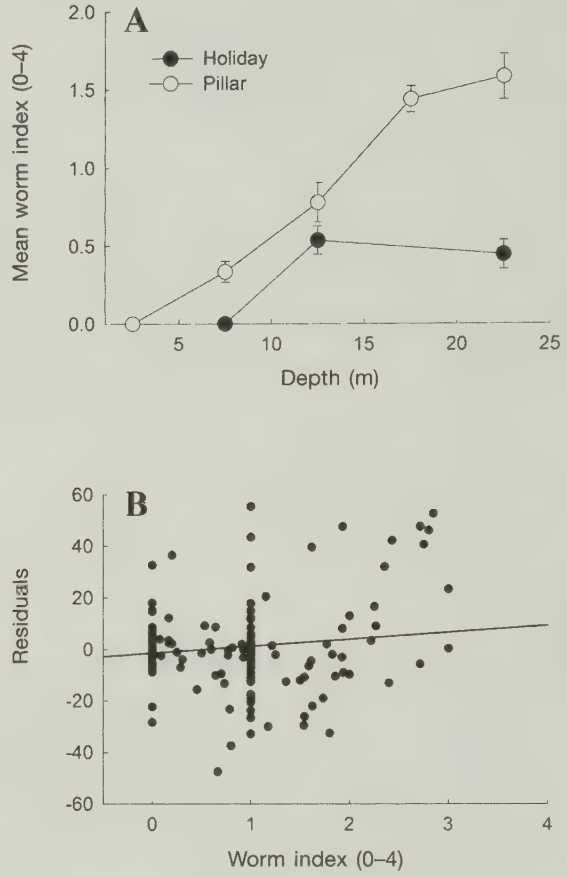

Figure 3

(**A**) Mean worm index scores (averaged over months), which provide a measure of relative abundance of worm tubes on a 5-point scale (0–4), plotted against depth for the sites at Holiday Beach and Pillar Creek Cove, Kodiak Island, Alaska, for surveys conducted in 2010. Error bars indicate standard error of the mean. (**B**) Residuals from generalized linear model analysis of crab density (without the worm index included as a covariate), plotted against worm index scores and indicating a positive relationship between crab and worm tube abundance after the confounding depth effect had been removed.

July, then decreased from July to August (Fig. 2, A and B). The density of age-0 Tanner crabs was strongly influenced by depth; crabs were generally absent from depths <8 m. At depths greater than 8 m, crab density rose with increasing depth. There was a significant interactive effect of depth and site; crabs were distributed more deeply at Pillar Creek Cove than at Holiday Beach (GLM depth×site: Wald χ^2=8.01, df=3, P=0.045). The depth effect also varied among months, with a more uniform distribution across depths in August as overall density decreased (depth×month: Wald χ^2=55.1, df=12, P<0.001). Crab density was generally higher at Pillar than at Holiday, although the magnitude of this dif-

ference varied somewhat between months (site×month: Wald $\chi 2=12.9$, df=3, $P=0.005$).

We conducted limited beam trawl sampling at Pillar during July and August, including depths beyond those attempted with the scrape (Fig. 2C). The depth distribution of crabs differed between July and August (Wald $\chi^2=17.1$, df=6, $P=0.009$). During July, crab density increased from the shallows to a peak at 25–35 m, declining farther offshore. By August, crab density was more uniform across depths as overall density decreased.

Worms tubes, principally those of *S. sibirica*, were generally more abundant at Pillar than at Holiday (Fig. 3A). At both sites, tubes were rare in the shallows but increased in abundance with depth. Therefore, the depth distribution of age-0 Tanner crabs mirrored the distribution of worm tubes. Abundance of worm tubes had a significant positive influence on crab density (Wald $\chi^2=233.1$, df=1, $P<0.001$). To graphically demonstrate this association, we performed a second GLM analysis, leaving out the worm covariate, and plotted the residuals against the worm index (Fig. 3B).

Crab densities were lower in 2011 than in 2010. With the addition of Womens and Kalsin sites in 2011, differences between study sites also became more evident (Fig. 4, A–D). Beyond the obvious difference in the overall abundance of crabs, perhaps most noticeable was the influence of site on depth distribution (Wald $\chi^2=56.0$, df=8, $P<0.001$). As in 2010, crab density at Holiday and Pillar consistently was highest at the greatest depth. In contrast, at Womens and Kalsin, crabs were found at shallower depths and more evenly distributed among depths. There was also an interactive effect wherein depth distribution differed among months (depth×month: Wald $\chi^2=17.4$, df=9, $P=0.043$). This effect was manifest as a "flattening" of the depth distribution curves, particularly during August at Holiday and Pillar—an effect similar to that observed during 2010.

Seasonal, or month to month, changes in crab density also differed among sites (month X site: Wald $\chi^2=27.4$, df=9, $P=0.001$). Most notable were changes in crab density subsequent to the end of settlement in July. Post-hoc comparisons indicated that mean crab density (crabs/m^2) declined from July to August at Holiday (July: 0.61 [standard error (SE) 0.18]; August: 0.26 [SE 0.09]; Wald $\chi^2=59.0$, df=3, $P<0.001$), as well as at Pillar (July: 0.66 [SE 0.25]; August: 0.15 [SE 0.07]; Wald $\chi^2=62.4$, df=3, $P<0.001$) and Kalsin (July: 0.34 [SE 0.07]; August: 0.20 [SE 0.05]; Wald $\chi^2=12.8$, df=3, $P=0.005$). In contrast, there was no decline in crab density from July to August at Womens (July: 0.11 [SE 0.02]; August: 0.12 [SE 0.02]; Wald $\chi^2=4.6$, df=1, $P=0.201$). There was no significant 3-way interactive effect of site, month, and depth on crab density (Wald $\chi^2=25.4$, df=18, $P=0.115$).

Results from beam trawl sampling (Fig. 5) indicate that, unlike in July 2010 when crabs were most dense at intermediate depths (25–35 m), crab density during 2011 was highest in the deepest tows (Wald $\chi^2=17.0$, df=4, $P=0.002$). Although crab density decreased from

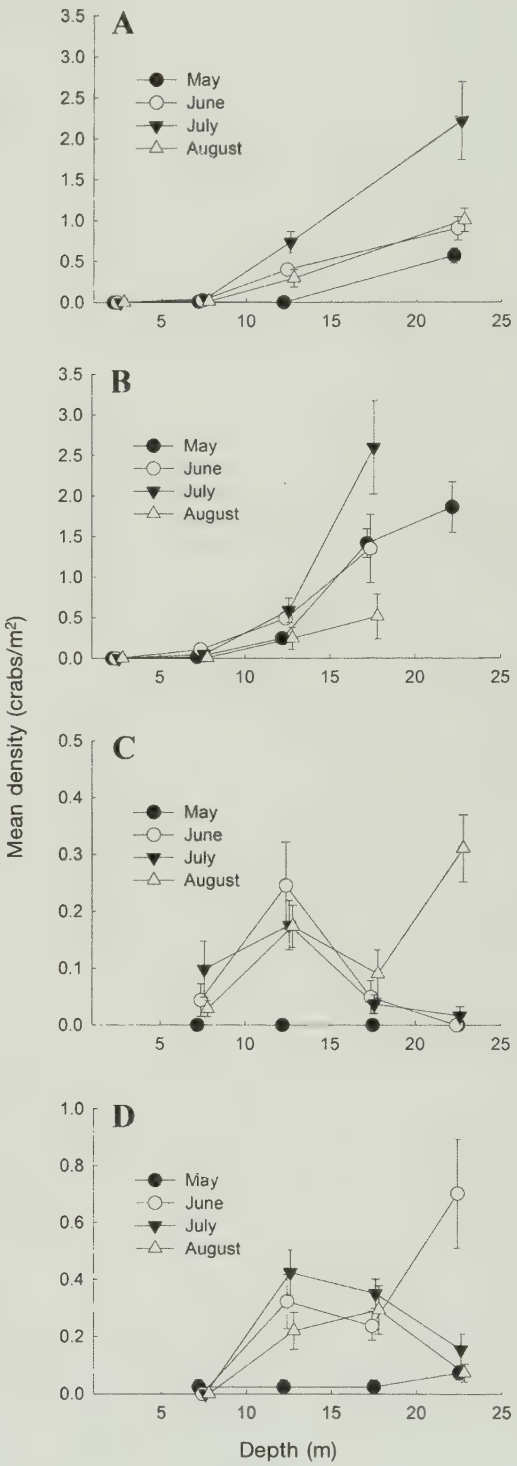

Figure 4

Mean densities of age-0 southern Tanner crabs (*Chionoecetes bairdi*), plotted against depth, determined from scrape tows conducted at (**A**) Holiday Beach, (**B**) Pillar Creek Cove, (**C**) Womens Bay, and (**D**) Kalsin Bay around Kodiak Island, Alaska, in the months of May–August 2011. Error bars indicate standard error of the mean.

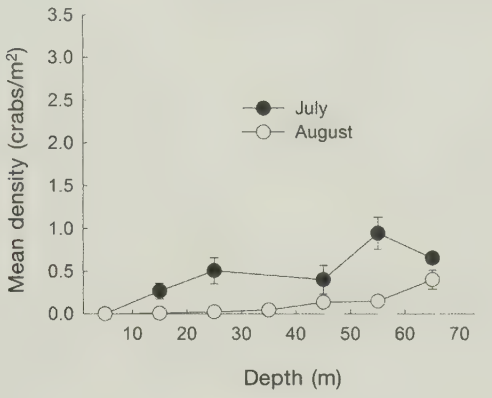

Figure 5

Mean densities of age-0 southern Tanner crabs (*Chionoecetes bairdi*) from beam trawl hauls, by depth, conducted at Pillar Creek Cove, Kodiak Island, Alaska, in July and August 2011. Error bars indicate standard error of the mean.

July to August (Wald χ^2=23.4, df=1, P<0.001), the effect of depth on density was consistent across months (month×depth: Wald χ^2=7.1, df=3, P=0.055).

At Holiday and Pillar, the depth distribution of polychaete worms in 2011 (Fig. 6) was similar to that observed in 2010 (Fig. 3), albeit, overall worm abundance was lower. Worms at Kalsin displayed a distribution similar to that of worms at Pillar, in distinct contrast to Womens, where worms were most abundant at the shallowest depth and decreased in abundance as depth increased. On first examination, worm abundance might be construed as influencing the distribution of crabs at Womens because crabs also were more abundant in shallow water. However, worm abundance did not have a significant influence on crab abundance in the GLM (Wald χ^2=3.0, df=1, P=0.083).

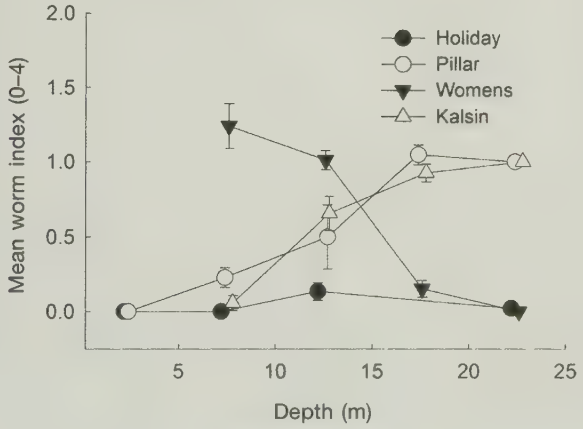

Figure 6

Mean worm index scores (averaged over months), which provide a measure of relative abundance of worm tubes on a 5-point scale (0–4), plotted against depth for each of the 4 sites surveyed in 2011 around Kodiak Island, Alaska, at Holiday Beach, Pillar Creek Cove, Womens Bay, and Kalsin Bay. Error bars indicate standard error of the mean.

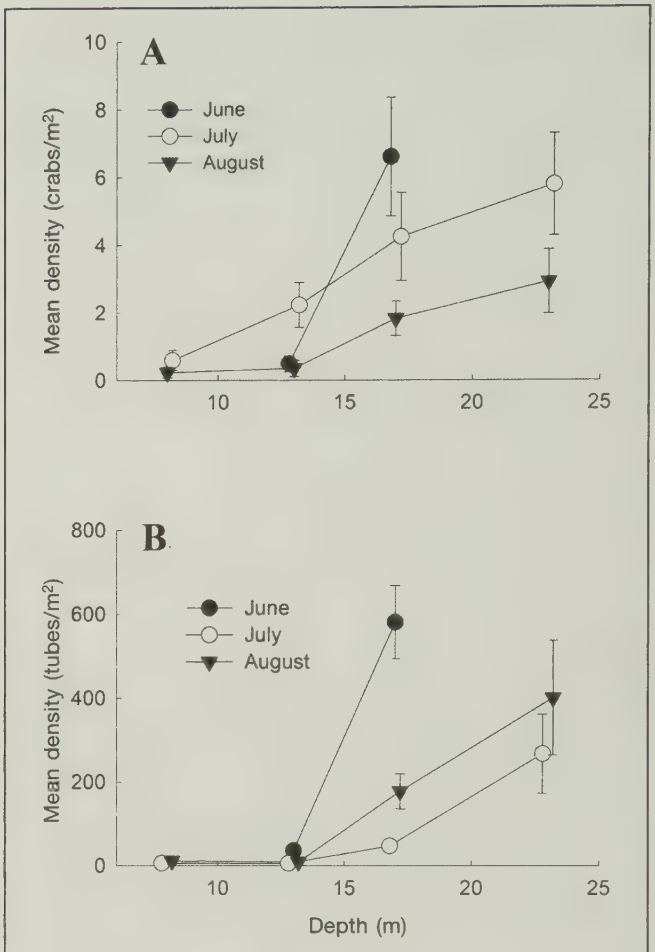

Figure 7

From quadrat surveys conducted by divers in 2010, mean densities (**A**) of age-0 southern Tanner crabs (*Chionoecetes bairdi*) and (**B**) of worm tubes, plotted against depth for the study site at Pillar Creek Cove, Kodiak Island, Alaska (*y*-axis variables are averaged over months). Error bars indicate standard error of the mean

Diver estimation of crab density

The quadrats used by divers to assess crab density during 2010 provided an examination of habitat associations on a micro scale (<1 m); the crab scrape, on the other hand, provided an examination at a larger scale (>10 m). Although there was a tendency for crab density from quadrats (Fig. 7A) to decline through the summer, this effect was not significant (Wald χ^2=5.3,

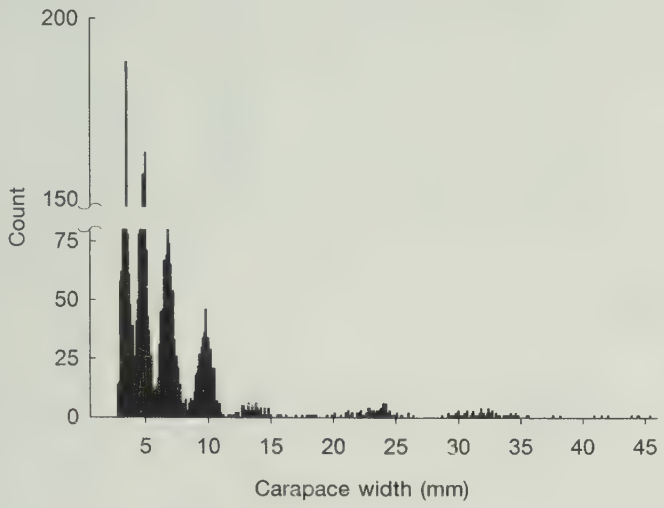

Figure 8

Cumulative size-frequency distribution of southern Tanner crabs (Chionoecetes bairdi) from all sites, months, and depths surveyed in 2010 and 2011 around Kodiak Island, Alaska. A tabulation of median size, size range, and molt increment for each molt stage is provided in Table 1.

df=2, P=0.070). As seen in the scrape data, crab density estimated by divers in quadrat surveys increased with depth (Wald χ^2=12.8, df=3, P=0.005). This depth effect was consistent over months (month×depth: Wald χ^2=3.5, df=4, P=0.474). Although crab density appeared to mirror the observed depth distribution of worm tubes (Fig. 7B), worms tubes were not a significant covariate in the GLM analysis (Wald χ^2=0.9, df=1, P=0.354), indicating no association at this spatial scale.

Table 1

Medians and ranges of carapace widths (mm) for proposed molt stages of southern Tanner crabs (*Chionoecetes bairdi*) collected during 2010 and 2011 from all 4 sites that were surveyed around Kodiak Island, Alaska. Increment percentages indicate the relative increase in carapace width from one molt stage to the next.

Stage	Median (mm)	Range (mm)	Increment (%)
C1	3.4	2.6–4.1	–
C2	4.8	4.2–5.6	41
C3	6.8	5.7–8.2	42
C4	9.7	8.3–11.3	43
C5	13.4	11.4–15.2	38
C6	17.8	15.3–20.1	32
C7	23.4	20.4–26.6	31
C8	31.8	28.5–35.6	36
C9	42.0	37.3–45.7	32

Age-0 crab molt intervals and size distributions

Cumulative size-frequency distributions (all sites and months) were examined initially for each year (2010 and 2011). However, because patterns were identical, we combined both years into a single distribution (Fig. 8; Table 1). Break points between peaks in the size-frequency distribution were taken to be boundaries between successive molt stages. Percent increase in size over the prior stage averaged 36.9%, within a range of 31–43% (Table 1). There was a trend for molt increments to decrease in later molt stages. Using this classification, we assigned individual crabs to stages, thereby allowing us to examine differences in population composition between months and study sites.

A comparison of the 4 study sites surveyed in August of 2010 revealed a significant difference in molt-stage frequencies (χ^2=349.13, df=12, P<0.001). C4 instars were dominant at Womens and Kalsin, and C3 instars were dominant at Holiday and Pillar. Accordingly, the mean carapace widths of crabs at Womens (10.1 mm [SE 0.1]) and Kalsin (9.1 mm [SE 0.1]) were larger than those at Holiday (7.2 mm [SE 0.1]) and Pillar (7.0 mm [SE 0.1]; Kruskal-Wallis: P<0.001; multiple comparisons: P<0.05).

Examination of data from surveys conducted in 2011 revealed that differences between study sites in frequency distribution of molt stages were established relatively early in the late summer (Fig. 9). Differences in molt-stage composition between sites were evident in May (χ^2=41.36, df=6, P<0.001). C1 instars dominated populations, although C2, C3, and even C4 instars were present at Kalsin and in lessening degrees at Pillar and Holiday (we did not include Womens in our analysis because only several C1 instars were encountered there). As a consequence, the mean carapace widths of crabs at Kalsin (4.5 mm [SE 0.2]) and Pillar (4.0 mm [SE 0.1]) were larger than the mean at Holiday (3.6 mm [SE 0.1]; Kruskal-Wallis: P<0.001; multiple comparisons: P<0.05). By June, crabs were present at Womens and were typically one stage further along than those at the other sites (χ^2=184.89, df=9, P<0.001). Accordingly, the mean carapace width of crabs at Womens (5.7 mm [SE 0.2]) was larger than the means for crabs at Kalsin (4.2 mm [SE 0.1]) and Pillar (3.8 mm [SE 0.1]), where crabs in turn were larger than crabs at Holiday (3.5 mm [SE 0.1]; Kruskal-Wallis: P<0.001; multiple comparisons: P<0.05). Similarly, in July, C3 instars were prevalent at Womens, whereas C2 instars dominated the other sites (χ^2=436.06, df=12, P<0.001). As a result, the order of mean carapace widths of crabs at the study sites was Womens > Kalsin > Holiday > Pillar, and all sites differed significantly from each other (Kruskal-Wallis: P<0.001; multiple comparisons: P<0.05). Lastly in August, C4 instars dominated at Womens, a mixture of C3 and C4 instars dominated at Kalsin, C3 instars were dominant at Holiday, and a

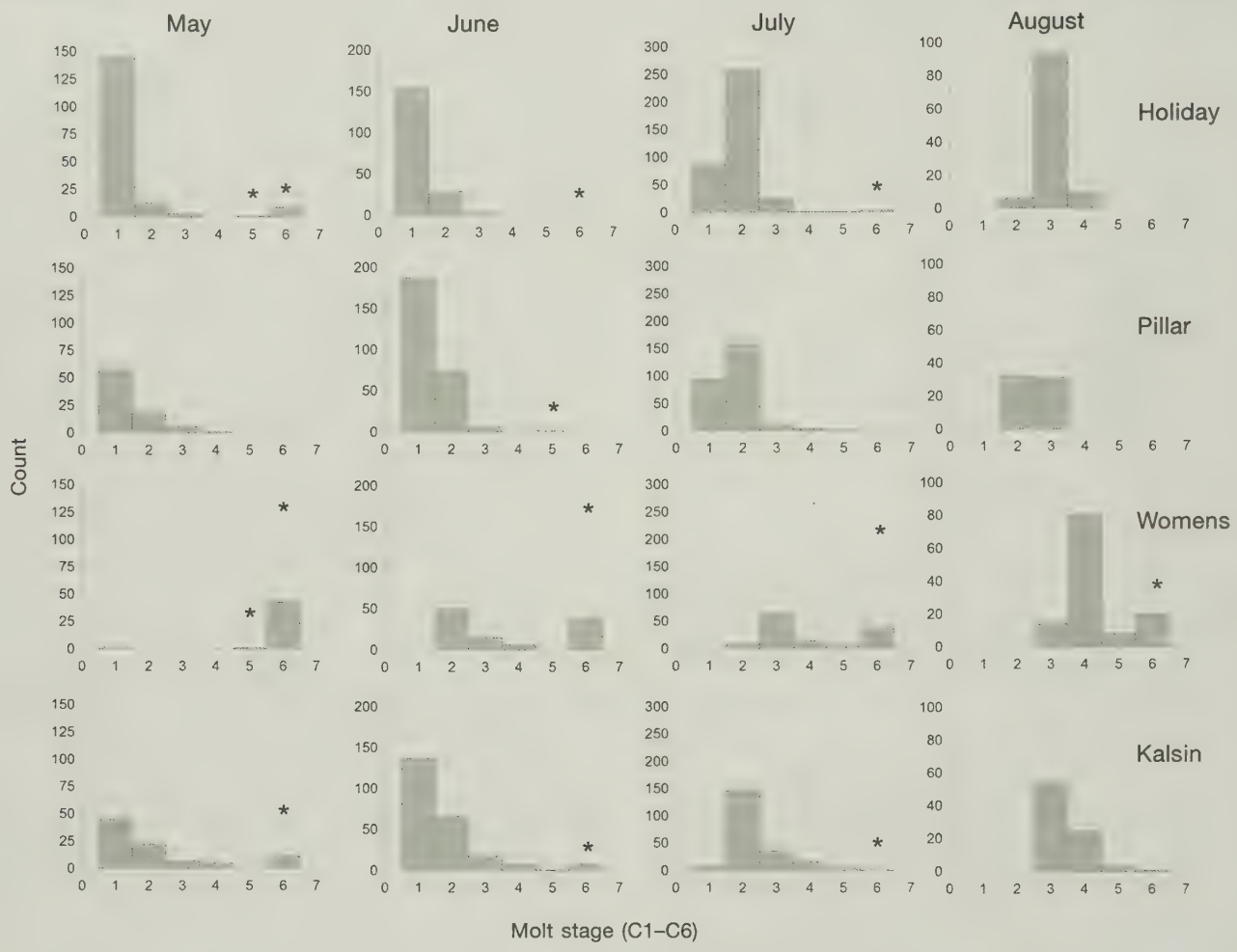

Figure 9

Frequency distribution of molt stages of southern Tanner crabs (*Chionoecetes bairdi*) from each of the 4 sites around Kodiak Island, Alaska, that were surveyed during May, June, July, and August 2011. An asterisk (*) indicates presumed age-1 crabs, which were excluded from statistical analysis. Columns are months (May–August). Rows are sites (Holiday Beach, Pillar Creek Cove, Womens Bay, Kalsin Bay). Note that the *y*-axes are different among months.

mixture of C2 and C3 instars were dominant at Pillar (χ^2=291.00, df=12, P<0.001). As in July, the ranking of sites by mean carapace width was Womens > Kalsin > Holiday > Pillar, and all sites differed significantly from each other (Kruskal-Wallis: P<0.001; multiple comparisons: P<0.05). Molt-stage composition varied with the interaction of month, depth, and study site; however, there was no discernible pattern, and, therefore, we did not explore this interactive effect further.

Although the relative abundance of molt stages largely controlled differences in mean carapace width among sites, for crabs at given molt stages there were also small but significant differences between sites. Considering only C1 crabs, we found that there was no difference in mean carapace width between sites ($F_{[3,\ 928]}$=1.34, P=0.261). However, among C2 crabs, mean carapace width was greater at Womens (4.93 mm [SE 0.03]) than at Kalsin (4.82 mm [SE 0.02]) and Holiday (4.78 mm [SE 0.02]), where the means in turn were larger than the mean at Pillar (4.70 mm [SE 0.02]); Kruskal-Wallis: P<0.001; multiple comparisons: P<0.05). Among C3 instars, those at Womens (7.13 mm [SE 0.04]) and Kalsin (6.98 mm [SE 0.03]) had greater mean carapace widths than those at Holiday (6.67 mm [SE 0.03]), where the mean in turn was larger than the mean at Pillar (6.55 mm [SE 0.03]); Kruskal-Wallis: P<0.001; multiple comparisons: P<0.05). Lastly, among C4 instars, those at Womens (9.77 mm [SE 0.03]) and Kalsin (9.82 mm [SE 0.05]) again had greater mean carapace widths than those at Holiday (9.51 mm [SE 0.08]), where the mean was in turn greater than that at Pillar (9.08 mm [SE 0.09]); $F_{[3,\ 503]}$=26.6, P<0.001). Crabs in the C5 and C6 molt stages were too few in number to provide meaningful comparisons.

Mean daily seawater temperatures at 15 m (MLLW) for the period from 20 May through 22 August 2011, were 8.2°C, 8.1°C, 8.0°C and 7.7°C for Womens, Pillar, Holiday, and Kalsin, respectively. Mean daily seawater temperature increased though the season ($F_{[1, 375]}$=7475.21, P<0.001) and differed among sites ($F_{[3, 375]}$=31.95, P<0.001), with mean temperature at Womens and Pillar higher than that at Holiday and with mean temperature at Holiday higher than at Kalsin (Tukey's HSD: P<0.05).

Discussion

Our results illuminate several aspects of the early life history and habitat use of recently settled Tanner crab. First, data indicate that settlement and metamorphosis by Tanner megalopae in the northwestern Gulf of Alaska begins in April and continue into July. We did not sample before May; therefore, our inference that settlement begins in April is based on the observation that in May nearly all age-0 Tanner crabs at our study sites were in the C1 molt stage, indicating that they had been on bottom for a relatively short period. By July, C1 instars were infrequent in scrape tows and were completely absent in August. This recruitment schedule resulted in increasing crabs densities from May to a peak in July, and it is consistent with the pattern of egg hatching (April–May) that has been reported for both primiparous and multiparous females (Stevens, 2003b; Swiney, 2008). Because the timing of settlement at our various sites was comparable and the 4 sites are separated by only tens of kilometers, we posit that larval sources for these sites were the same. Stevens (2003b) speculated that hatching of Tanner eggs in Chiniak Bay is synchronized with spring tides, which act to break down dominant costal circulation patterns and potentially result in greater larval retention within the Chiniak Bay system.

Depth had a strong influence on crab density, although this effect varied between embayments. At Pillar and Holiday, recently settled crabs were absent or scarce from scrape tows at depths <8 m, but they became more abundant with increasing depth out to 23 m. Trawl tows conducted during July 2010 at Pillar revealed that crab density was highest at depths of 30–35 m, decreasing farther offshore, at depths of 50–80 m. By August, densities had declined and there was no longer a maxima at intermediate depths. In contrast with densities at Pillar and Holiday, at Womens and Kalsin, crab density was generally highest at depths between 10 and 15 m, although there was variability among months. We did not conduct trawl sampling at either Womens or Kalsin and have no knowledge of what crab densities were at depths greater than those sampled by the scrape (25 m).

We suspect that the difference in crab depth distribution between Pillar and Holiday, on one hand, and Womens and Kalsin, on the other, is primarily related to wave energy. Womens is the most protected of the study sites, with a narrow entrance and offshore islands that dissipate wave energy. Although not as protected as Womens, the Kalsin study site is located near the head of the Kalsin Bay and, as such, typically experiences lower wave action than the sites at Pillar and Holiday. Pillar and particularly Holiday are more exposed and frequently experience strong wave action from the Gulf of Alaska. Although bottom surge associated with wave action may directly affect crabs, by interfering with settlement, impeding foraging, or dislodging crabs from the bottom, we suspect that the influence of wave energy on sediment characteristics is also a primary factor.

Because of the inverse relationship between depth and wave-induced bottom scour, sites such as Pillar and Holiday are characterized by coarse sand in shallow water (depths <10 m), by fine sands or silty sands at depths of 10–25 m, and finally by an increasing contribution of mud at depths >25 m (Stoner et al., 2007). At Womens and Kalsin, as a result of lower wave energy, compared with that at other sites, finer silts and muddy sediments occur at shallower depths (senior author, personal observ.). For juvenile Tanner crabs, the ability to bury themselves in silty or muddy sediments is their first line of defense against predators. Similarly, juvenile flatfish use burial as a predation deterrent and preferentially choose sediment in which they can easily bury themselves (Stoner and Ottmar, 2003). Furthermore, fine sediments around Kodiak typically have higher organic content than coarse sediment (Stoner et al., 2007). Tanner crabs consume not only a variety of infaunal prey, including bivalves, polychaetes, and other crustaceans, but also detrital material (Jewett and Feder, 1983), which presumably occurs in higher concentrations in silty and muddy sediments than in coarser sediments. After the spring bloom, diatoms settle to the bottom and accumulate in low wave-energy areas. This flocculent material is readily observed on the surface of fine sediment in Womens Bay during late spring and summer months (Munk[4]).

Juvenile crabs and fishes often seek physically structured habitats. Juvenile red king crab and blue king crab (*Paralithodes platypus*) prefer highly structured habitats, which consist of pebbles, cobble, hydroids, macroalgae, shell material, etc., where they are less vulnerable to predators (Stoner, 2009; Pirtle and Stoner, 2010). Tanner crabs, like snow crabs, generally are thought to prefer sandy, silty, and muddy sediments—a preference that might be explained by their lack of spines that would, if present as in king crabs, inhibit them from rapidly burying themselves (senior author, personal observ.). However, in beam trawl hauls conducted during 2009, we observed that recently settled Tanner crabs were most common at depths of 15–30 m, the same depth range where *S. sibirica* is most abundant (Ryer et al., 2013). On the basis of this re-

[4] Munk, E. 2008. Personal commun. Kodiak Laboratory, Alaska Fisheries Science Center, 301 Research Ct., Kodiak, AK 99615.

lationship, we hypothesized that recently settled Tanner crabs were preferentially using the habitat created by *S. sibirica*. Juvenile flatfish, principally northern rock sole and Pacific halibut (*Hippoglossus stenolepis*), are also attracted to this type of habitat (Ryer et al., 2013). Although fish avoid areas where worms were so dense as to preclude burial, fish aggregate along the sparse and patchy edges of this habitat type (Ryer et al., 2013). In 2010, when both worm tubes and crabs were relatively abundant, there was a significant positive effect of worm abundance on crab density, after the effect of depth was factored out. However, during 2011, when both worms and crabs were less abundant, worm abundance had no effect on crab density. This difference in effects indicates that the habitat created by *S. sibirica* tubes has only a modest influence on distribution of age-0 Tanner crabs.

In a manner analogous to the refuge function of eelgrass (*Zostera marina* L.) (Wilson et al., 1987; Ryer, 1988), the physical structure of the worm tube habitat may provide age-0 Tanner crabs refuge from fish predators. Predation by Pacific cod (*Gadus macrocephalus*) is thought to regulate Tanner crab recruitment in the Gulf of Alaska and Bering Sea (Livingston, 1989). Juvenile Tanner crabs may also consume *S. sibirica* directly or the associated invertebrate species supported by the worm tube habitat (senior author, personal observ.). Alternatively, both species may be attracted to the same depth and sediment characteristics, possibly explaining their association. This interpretation is supported by results from our quadrat surveys, which were conducted by divers at a finer scale than that of the scrape tows and which indicated there was no relationship between crab density and worm tube density. Resolving the nature of this association could be addressed though controlled laboratory experimentation that might reveal whether age-0 Tanner crabs show an attraction for the structure provided by *S. sibirica* and whether an association reduces predation on age-0 Tanner crabs.

Growth in crustaceans is a function of molt increments, typically expressed as percent increase in size, and a function of the frequency with which those molts occur. Knowledge of the age distribution of a population can be important information in stock assessment. In practice, aging commercially harvested North Pacific crabs species relies upon imprecise estimates of the number of molts that occur during each year. Our data indicate that age-0 Tanner crab, around Kodiak Island, pass through between 3 and 5 molts from settlement through August. By May of the next year, crabs have gone through 6 or more molt stages. Although no other studies have documented growth during the first year for this species, Donaldson et al. (1981) reported a strong size mode at 18 mm (C6 instars) during May–June in Prince William Sound, northern Gulf of Alaska. Therefore, it appears that crabs in the northern Gulf of Alaska, including near Kodiak, typically go through roughly 6 molt stages in their first year. On the basis of various samples from areas in the Gulf of Alaska, these authors concluded that Tanner crabs typically undergo 3 more molts in their second year and 2 molts in their third year, after which molting occurs annually. Donaldson et al. (1981) found that 50% of females were mature at 83 mm and 50% males were mature at 90 mm, indicating that age at maturity for this species is approximately 5 years for females and 7 years for males.

Variance in this age-growth schedule will result from differential growth rates between localities and years. Temperature plays an important role in modulating growth in crustaceans (Hartnoll, 1982). After 60 days, red king crab and blue king crab reared at 1.5°C were mostly still C1 instars, whereas those reared at 8°C for 60 days were mostly C3 instars (Stoner et al., 2010, 2013). This finding indicates that crabs settling into habitats with differing ambient temperatures may experience vastly different growth rates. Using published, temperature-dependent growth rates, Stevens (1990) estimated growth and years to maturity for red king crabs from areas with varying temperature regimes in Bristol Bay, Alaska. He concluded that growth varies greatly between areas, such that crabs recruiting to the pot fishery in the eastern Bering Sea in any given year may be derived from up to 4 or 5 year classes. This conclusion indicates that it would be advantageous for Tanner megalopae to preferentially settle in shallower water where temperatures are supportive of accelerated growth. Naturally, such an outcome would require that other factors, such as forage base and predation risk, do not compromise the enhanced growth for crabs settling in shallower water.

Data from out study indicate that growth rates differ among sites. During both 2010 and 2011, crabs from Womens were generally 1 molt stage larger by the end of August than crabs from Pillar and Holiday. There are several possible explanations for this observed size difference. Crabs may simply recruit earlier at Womens than at the other sites. However, this notion is not consistent with results from our May 2011 sampling which indicated that crabs at Womens may actually have recruited slightly later. Temperature may play a role. We did document minor differences in mean ambient bottom temperature (at a depth of 15 m MLLW) between sites; temperature was greatest at Womens. However, the difference in mean temperature between sites was only 0.5°C, and we are skeptical that this difference would result in the greater size observed for crabs at Womens. Age-0 Tanner crabs molt approximately once every 873 degree days in the laboratory, and a temperature shift of 0.5°C would only marginally increase the frequency of molting (Long et al., 2013b). Furthermore, temperature was lowest at Kalsin, yet crabs at Kalsin were closest in size to those at Womens and generally were larger than those at Pillar and Holiday. It is perhaps more important to note that bottom temperature at 15 m may not be representative of temperatures for an entire embayment. For example, at both Womens and Kalsin where high growth was seen, crabs tended to be found at shallower depths, where temperatures are expected to be higher.

The observed difference in molt-stage frequency between sites may be a product of differential emigration or mortality. If predation is size-dependent, and predators are largely consuming smaller crabs, the size-frequency distribution of crabs at Womens could be skewed toward larger crabs by heavy predation. If this size-selective postsettlement process was in fact occurring, we would expect crab numbers to decline rapidly as a result of predation. Settlement was largely complete by July, but Womens was the only site to experience no population decline from July to August, indicating that predation was low at that site. Alternatively, differential migration may offer an explanation, if it is a natural progression for Tanner crabs to settle in shallow water and then migrate to deeper water. Unlike the other sites, Womens has a narrow entrance with a sill that rises up to a depth of approximately 11 m. This narrow entrance could reduce offshore migration of juveniles in Womens Bay. However, there is no structural hindrance to offshore migration at Kalsin, where crabs were also relatively large. If anything, we suspect that the shallow sill at Womens may block the offshore migration of larger crabs in the fall, winter, or spring because Womens was the only site that retained an appreciable number of age-1 crabs.

Lastly, sites like Womens and Kalsin have finer sediments, which are likely to accumulate organic carbon and support a denser infaunal community than the other sites. Therefore, crabs may have more or better food there. Results of preliminary lipid and essential fatty acid analysis that we performed on crabs from our study sites (Copeman and Ryer[5]) indicate that crabs from Womens and Kalsin had higher levels of storage lipids and of diatom fatty acid markers than crabs from Pillar and Holiday. Overall higher levels of storage lipids and diatom-derived fatty acids have been associated with accelerated growth in larval Pacific cod (Copeman and Laurel, 2010) and juvenile red king crabs (Copeman et al., 2012).

We also observed that, for individual molt stages, crabs were larger at Womens and Kalsin than at Holiday and Pillar. In a review of crustacean growth, Hartnoll (1982) concluded that, for many species, increases in the quantity or quality of food not only decreased the intermolt period but also increased the molt increment. However, this effect of food availability on growth may vary ontogenetically. Among larger juvenile blue crabs, growth has been correlated with higher food density (Seitz et al., 2005), whereas, for smaller juveniles, this link has not been made (Long et al., 2011). In contrast, increases in temperature typically decrease both the intermolt period the molt increment, although Stoner et al. (2010) reported an increase in red king crab molt increments with increased temperature. A further understanding of the relative role of temperature versus food on growth of the Tanner crab will await controlled laboratory experiments that manipulate these parameters.

Whether juvenile Tanner crabs use habitats that are distinct from those occupied by adults remains unclear. The arguments presented here make the case that juveniles would fare better in shallow waters (depths <50 m). Further, we encountered few individuals larger than the C7 molt stage (carapace widths of 20–26 mm), indicating that crabs older than 2 or 3 years of age are found in different, perhaps, deeper habitats. In Glacier Bay, Alaska, Tanner crabs are segregated by ontogenetic stage; smaller, or juvenile, crabs are located at the heads of fjords, near glaciers, and adult, or larger crabs are more centrally located in fjords and in inlet areas (Nielsen et al., 2007). However, this segregation did not appear to be depth related, and the authors speculated that cannibalism, competition, predation, or differences in substrate preferences might be responsible. In Cook Inlet, Alaska, large individuals were found throughout the inlet, whereas juveniles with carapace widths <20 mm were concentrated in the inlet mouth at generally greater depths (Paul, 1982). This diversity of results indicates that the factors that control the distribution of age-0 crabs can vary between areas.

Although we do not yet know the full range of depths and habitats used by age-0 Tanner crabs, the settlement densities and patterns documented in this work indicate that relatively shallow waters (<50 m) may constitute an important habitat for Tanner crabs around Kodiak Island, particularly because temperatures in these shallow waters can be expected to speed growth and shorten the number of years before crabs recruit to the fishable or reproductive population.

[5] Copeman, L. A., and C. H. Ryer. 2010. Unpubl. data. Alaska Fisheries Science Center, 2030 S. Marine Science Dr., Bldg. RSF951, Newport, OR 97365-5296.

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Literature cited

Baker, R., and M. Sheaves.
2007. Shallow-water refuge paradigm: conflicting evidence from tethering experiments in a tropical estuary. Mar. Ecol. Prog. Ser. 349:13–22.

Conover, W. J.
1971. Practical nonparametric statistics, 462 p. John Wiley & Sons, Inc., New York.

Copeman, L. A., and B. J. Laurel.
2010. Experimental evidence of fatty acid limited growth

and survival in Pacific cod larvae. Mar. Ecol. Prog. Ser. 412:259–272.

Copeman, L. A, A. W. Stoner, M. L. Ottmar, B. Daly, C. C. Parrish, and G. L. Eckert.
2012. Total lipids, lipid classes, and fatty acids of newly settled red king crab (*Paralithodes camtschaticus*): comparison of hatchery-cultured and wild crabs. J. Shellfish Res. 31:153–165.

Cushing, D. H.
1975. Marine ecology and fisheries, 278 p. Cambridge Univ. Press, Cambridge, MA.

Donaldson, W. E., R. T. Cooney, and J. R. Hilsinger.
1981. Growth, age and size at maturity of Tanner crab, *Chinoecetes bairdi* M. J. Rathbun, in the northern Gulf of Alaska (Decapoda, Brachyura). Crustaceana 40:286–302. [Available at http://www.jstor.org/stable/20103618.]

Etherington, L. L., and D. B. Eggleston.
2003. Spatial dynamics of large-scale, multistage crab (*Callinectes sapidus*) dispersal: determinants and consequences for recruitment. Can. J. Fish. Aquat. Sci. 60:873–887.

Hartnoll, R. G.
1982. Growth. *In* The biology of crustacea, vol. 2: morphology, embryology, and genetics. (L. G. Abele, ed.), p.111–196. Academic Press, New York.

Heck, K. L., L. D. Coen, and S. G. Morgan.
2001. Pre- and post-settlement factors as determinants of juvenile blue crab *Callinectes sapidus* abundance: results from the north-central Gulf of Mexico. Mar. Ecol. Prog. Ser. 222:163–176.

Hurst, T. P., and A. A. Abookire.
2006. Temporal and spatial variation in potential and realized growth rates of age-0 year northern rock sole. J. Fish. Biol. 68:905–919.

Jewett, S. C., and H. M. Feder.
1983. Food of the Tanner crab *Chionoecetes bairdi* near Kodiak Island, Alaska. J. Crust. Biol. 3:196–207. [Available at http://www.jstor.org/stable/1548256.]

Linehan, J. E., R. S. Gregory, and D. C. Schneider.
2001. Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. J. Exp. Mar. Biol. Ecol. 263:25–44.

Livingston, P. A.
1989. Interannual trends in Pacific cod, *Gadus macrocephalus*, predation on three commercially important crab species in the eastern Bering Sea. Fish. Bull. 87:807–827.

Loher, T., and D. A. Armstrong.
2000. Effects of habitat complexity and relative larval supply on the establishment of early benthic phase red king crab (*Paralithodes camtschaticus* Tilesius, 1815) populations in Auke Bay, Alaska. J. Exp. Mar. Biol. Ecol. 245:83–109.

Long, W. C., J. N. Grow, J. E. Majoris, and A. H. Hines.
2011. Effects of anthropogenic shoreline hardening and invasion by *Phragmites australis* on habitat quality for juvenile blue crabs (*Callinectes sapidus*). J. Exp. Mar. Biol. Ecol. 409:215–222.

Long, W. C., A. J. Sellers, and A. H. Hines.
2013a. Mechanism by which coarse woody debris affects predation and community structure in Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 446:297–305.

Long, W. C., K. M. Swiney, C. Harris, H. N. Page, and R. J. Foy.
2013b. Effects of ocean acidification on juvenile red king crab (*Paralithodes camtschaticus*) and Tanner crab (*Chionoecetes bairdi*) growth, condition, calcification, and survival. PLoS One 8(4):e60959.

Manderson, J. P., J. Pessutti, J. G. Hilbert, and F. Juanes.
2004. Shallow water predation risk for a juvenile flatfish (winter flounder; *Pseudopleuronectes americanus*, Walbaum) in a northwest Atlantic estuary. J. Exp. Mar. Biol. Ecol. 304:137–157.

Nielsen, J. K, S. J. Taggart, T. C. Shirley, and J. Mondragon.
2007. Spatial distribution of juvenile and adult female Tanner crabs (*Chionoecetes bairdi*) in a glacial fjord excosystem: implications for recruitment processes. ICES J. Mar. Sci. 64:1772–1784. Orensanz, J. M., J. Armstrong, D. Armstrong, and R. Hilborn.
1998. Crustacean resources are vulnerable to serial depletion—the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. Rev. Fish Biol. Fish. 8:117–176.

Paul, D. M.
1982. Distribution of juvenile *Chionoecetes bairdi* in Cook Inlet. *In* Proceedings of the international symposium on the genus *Chionoecetes*, p. 173–190. Alaska Sea Grant Rep. 82-10. Alaska Sea Grant College Program, Univ. Alaska, Fairbanks, AK.

Pirtle, J. L., and A. W. Stoner.
2010. Red king crab (*Paralithodes camtschaticus*) early post-settlement habitat choice: Structure, food, and ontogeny. J. Exp. Mar. Biol. Ecol. 393:130–137.

Rosenkranz, G. E., A. V. Tyler, G. H. Kruse, and H. J. Niebauer.
1998. Relationship between wind and year class strength for Tanner crabs in the southeastern Bering Sea. Alaska Fish. Res. Bull. 5:18–24.

Ryer, C. H.
1988. Pipefish foraging: the effects of fish size, prey size and altered habitat complexity. Mar. Ecol. Prog. Ser. 48:37–45.

Ryer, C. H., M. L. Spencer, P. Iseri, B. A. Knoth, B. J. Laurel, and A.W. Stoner.
2013. Polychaete worm tubes modify juvenile northern rock sole *Lepidopsetta polyxystra* depth distribution in Kodiak nurseries. J. Exp. Mar. Biol. Ecol. 446:311–319.

Ryer, C. H., K. S. Boersma, and T. P. Hurst.
2012. Growth and distributional correlates of behavior in three co-occurring juvenile flatfishes. Mar. Ecol. Prog. Ser. 460:183–193.

Ryer, C. H., B. J. Laurel, and A. W. Stoner.
2010. Testing the shallow water refuge hypothesis in flatfish nurseries. Mar. Ecol. Prog. Ser. 415:275–282.

Ryer, C. H., A. W. Stoner, M. L. Spencer, and A. A. Abookire.
2007. Presence of larger flatfish modifies habitat preference by Age-0 northern rock sole *Lepidopsetta polyxystra*. Mar. Ecol. Prog. Ser. 342:227–238.

Ryer, C. H., A. W. Stoner, and R. H. Titgen.
2004. Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. Mar. Ecol. Prog. Ser. 268:231–243.

Seitz, R. D., R. N. Lipcius, and M. S. Seebo.
2005. Food availability and growth of the blue crab in seagrass and unvegetated nurseries of Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 319:57–68.

Sogard, S. M.
1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60:1129–1157.
Sokal, R. R., and F. J. Rohlf.
1969. Biometry: the principles and practice of statistics in biological research, 776 p. W. H. Freeman and Company, San Francisco.
Spencer, M. L., A. W. Stoner, C. H. Ryer, and J. E. Munk.
2005. A towed camera sled for estimating abundance of juvenile flatfishes and habitat characteristics: Comparison with beam trawls and divers. Estuar. Coast. Shelf Sci. 64:497–503.
Stevens, B. G.
1990. Temperature-dependent growth of juvenile red king crab (*Paralithodes camtschatica*) and its effects on size-at-age and subsequent recruitment in the eastern Bering Sea. Can. J. Fish. Aquat. Sci. 47:1307–1317.
2003a. Settlement, substratum preference, and survival of red king crab *Paralithodes camtschaticus* (Tilesius, 1815) glaucothoe on natural substrata in the laboratory. J. Exp. Mar. Biol. Ecol. 283:63–78.
2003b. Timing of aggregation and larval release by Tanner crabs, *Chionoecetes bairdi*, in relation to tidal current patterns. Fish. Res. 65:201–216.
Stoner, A. W.
2009. Habitat-mediated survival of newly settled red king crab in the presence of a predatory fish: Role of habitat complexity and heterogeneity. J. Exp. Mar. Biol. Ecol. 382:54–60.
Stoner, A. W., L. A. Copeman, and M. L. Ottmar.
2013. Molting, growth, and energetics of newly-settled blue king crab: Effects of temperature and comparisons with red king crab. J. Exp. Mar. Biol. Ecol. 442:10–21.
Stoner, A. W., M. L. Ottmar, and L. A. Copeman.
2010. Temperature effects on molting, growth, and lipid composition of newly-settled red king crab. J. Exp. Mar. Biol. Ecol. 393:138–147.
Stoner, A. W., M. L. Spencer, and C. H. Ryer.
2007. Flatfish-habitat associations in Alaska nursery grounds: Use of continuous video records for multi-scale spatial analysis. J. Sea Res. 57:137–150.
Stoner, A. W., and M. L.Ottmar.
2003. Relationships between size-specific sediment preferences and burial capabilities in juveniles of two Alaska flatfishes. J. Exp. Mar. Biol. Ecol. 282:85–101.
Swiney, K. M.
2008. Egg extrusion, embryo development, timing and duration of eclosion, and incubation period of primiparous and multiparous Tanner crabs (*Chionoecetes bairdi*). J. Crust. Biol. 28:334–341. [Available at http://www.jstor.org/stable/20487736.]
Wahle, R. A., and R. S. Steneck.
1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? Mar. Ecol. Prog. Ser. 69:231–243.
Wald, A.
1943. Tests of statistical hypotheses concerning several parameters when the number of observations is large. Trans. Am. Math. Soc. 54:426–482.
Wilson, K. A., K. L. Heck, Jr., and K. W. Able.
1987. Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. Fish. Bull. 85:53–58.
Woodby, D., D. Carlile, S. Siddeek, F. Funk, J. H. Clark, and L. Hulbert.
2005. Commercial fisheries of Alaska. Alaska Dep. Fish Game Spec. Publ. 05–09, 66 p. [Available at http://www.adfg.alaska.gov/FedAidPDFs/sp05-09.pdf.]
Yamashita, Y., M. Tanaka, and J. M. Miller.
2001. Ecophysiology of juvenile flatfish in nursery grounds. J. Sea. Res. 45:205–218.

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Correlating environmental and biogenic factors with abundance and distribution of Pacific ocean perch (*Sebastes alutus*) in the Aleutian Islands, Alaska

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Abstract—In the Aleutian Islands, patterns of distribution and abundance of Pacific ocean perch (*Sebastes alutus*) are influenced by oceanographic processes and biogenic structures. We used generalized additive modeling (GAM) to examine relationships between these predictors and patterns of settled juvenile and adult distribution and abundance from bottom trawl surveys conducted from 1997 through 2010. Depth, temperature, and location had the greatest influence, and biogenic structures co-occurring with this species improved predictions. Model results confirmed previously reported depth- and temperature-dependent patterns of Pacific ocean perch and revealed the elevated presence and abundance of this fish in proximity to Aleutian passes. Adults were more common and abundant in deeper (~225 m) water than were juveniles (~150 m), and the probability of encountering either life stage increased in the presence of fan- and ball-shaped sponges over moderate slopes and decreased with increasing tidal velocities. The GAMs accounted for one-quarter of the deviance for juvenile presence–absence (24.9%) and conditional abundance (25.0%) and accounted for 38.7% and 42.5% of the deviance for the same adult response variables. Although depth, temperature, and location were the dominant predictor variables of both juvenile presence and abundance, our results indicate that biogenic structures that provide vertical structure in otherwise low-relief, trawlable habitats may represent refugia for Pacific ocean perch juveniles and adults.

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Describing essential fish habitat (EFH), defined by the Magnuson-Stevens Fishery Conservation and Management Act (Magnuson-Stevens Act) as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity," has been the focus of much recent habitat research. Laidig et al. (2009) used the *Delta* submersible to conduct visual surveys on the central California shelf and found that demersal fishes associated with boulder and cobble substrata occurred in greater numbers than they did with mud or brachiopod beds. Other studies have observed denser and more diverse assemblages of rockfishes in the presence of increased boulder coverage (Marliave and Challenger, 2009) or in association with rocky ridges (Rooper et al., 2010). Greene et al. (2011) demonstrated that rugged seafloor geomorphologies in southeast Alaska can be used to identify suitable habitat for demersal shelf rockfish (*Sebastes* spp.). Living substrata can also modify seafloor habitats in ways that impact EFH. Others have considered biogenic structures, such as sponges, corals, and bryozoans, to be important habitat-forming organisms in Alaska (Heifetz et al., 2005; Malecha et al., 2005; Stone et al., 2011) and other waters (e.g., Barthel, 1997 [Weddell Sea]; Beazley et al., 2013 [the northwest Atlantic]; and Coker et al., 2014 [warm-water coral reefs]). In this study, we attempt to add to the growing body of knowledge used to identify and describe EFH for species of *Sebastes* in Alaska.

The Resource Assessment and Conservation Engineering (RACE) Division of the NOAA Alaska Fisheries Science Center (AFSC) has conducted periodic bottom trawl surveys in the Aleutian Islands since 1980 (von Szalay et al., 2011). These surveys are designed to collect fisheries-independent data on the status and trends of fish and invertebrate species to support formal stock assessments. One of the most abundant commercially harvested species landed from trawl fisheries in the Aleutian Islands is the Pacific ocean perch (*Sebastes alutus*) (Zenger, 2004; Rooper and Wilkins, 2008; von Szalay et al., 2011), and Pacific ocean perch biomass from this region has been increasing over the last decade

(Spencer and Ianelli[1]). In addition to the commercially harvested species that are one focus of our groundfish surveys, we collect a large amount of biological and physical data that characterize the habitat where these animals are found.

Previous studies have related the distribution and abundance patterns of Pacific ocean perch to physical and biological oceanographic processes in Alaska waters. Logerwell et al. (2005) examined geographic patterns of demersal ichthyofauna in the Aleutian Islands and found that smaller Pacific ocean perch (≤25 cm, Reuter[2]) inhabited shallower water (<150 m) than that inhabited by larger individuals, and they further suggested that large catches (>100 kg/ha) could be affiliated with zones of increased productivity and prey availability. Other researchers have confirmed that juvenile and adult Pacific ocean perch occur over similar temperature ranges but present different depth distributions (i.e., adults inhabit >200 m waters) (Carlson and Haight, 1976; Rooper, 2008).

Epibenthic invertebrates, such as sponges, corals, and bryozoans, are common in the Aleutian Islands (Malecha et al., 2005), where they are collected regularly as part of the AFSC RACE Division bottom trawl surveys (Heifetz et al., 2005). Their extent and diversity also have been noted from submersible and underwater camera studies of the region (Rooper et al., 2007; Stone et al., 2011). Despite their apparent ubiquity in the Aleutian Islands, we presume that these attached sessile invertebrates are patchily distributed in the trawlable areas where RACE bottom trawl surveys are conducted. Mounting evidence indicates that the presence of sponges and corals enhances structural heterogeneity in otherwise low-relief environments and can lead to increases in biodiversity and abundance of associated animals (e.g., Tissot et al., 2006; Beazley et al., 2013; Knudby et al., 2013). The morphological features of these biogenic structures may also serve as refugia for different life stages of commercially harvested species of *Sebastes* (Freese and Wing, 2003; Rooper and Boldt, 2005; Baillon et al., 2012) and Atka mackerel (*Pleurogrammus monopterygius*) (Rand and Lowe, 2011) in Alaska waters.

Previous studies have also shown putative associations of rockfishes with sponge, coral, and bryozoan assemblages across a wide range of physical and oceanographic conditions (Love et al., 1991; Rooper and Martin, 2012). Other studies have shown that rockfishes in low-relief, trawlable habitats (e.g., sand or gravel bottom with few boulders or obstructions) tend to concentrate near the few boulders or rocky outcrops with attached epibenthic invertebrate communities (e.g., Freese and Wing, 2003; Du Preez and Tunnicliffe, 2011). The Pacific ocean perch has been the focus of several previous studies in Alaska, and there is strong evidence that postsettlement juveniles and adults of Pacific ocean perch are found associated with sponges and corals (Krieger, 1993; Brodeur, 2001; Rooper and Boldt, 2005; Rooper et al., 2007). These studies have not distinguished species of sponges, corals, or bryozoans because of the difficulty in providing consistent identifications. Our study attempts to determine whether the presence or absence of biogenic structures across the broad spectrum of environmental conditions under which they occur affects Pacific ocean perch distribution and abundance.

Consistent field identification of sponges to specific or even generic levels of classification is difficult with the macroscopic techniques available in the field. Adding to the confusion, sponge morphological features, even within a single species, can vary dramatically with environmental conditions, such as current flow and sedimentation rate (Dayton et al., 1974; Bell and Barnes, 2001; Stone et al., 2011), and sponges quickly adapt their morphology to their environment (Palumbi, 1984). Given these challenges, categorizing sponges into groups based on their gross morphology is an attractive alternative. The approach of lumping sponges into groups based on body form has the advantage of eliminating confusion caused by changing and differentially applied systematics and gives us an intuitive link to EFH. In this study, we consider sponge morphology from a functional perspective (the "fish-eye view") of the structure it provides in the habitat. An added benefit of grouping the sponges by this functional morphology is to foster comparability of sponge assemblages among survey years by downplaying the differences in identification attributable to differing levels of expertise among the field biologists.

Sponges and corals are vulnerable to removal or damage by fishing gear (Engel and Kvitek, 1998; Freese et al., 1999; Freese, 2001; Wassenberg et al., 2002; Stone et al., 2011). In addition, these sessile invertebrates are long lived and have limited larval dispersal and reproductive potential (Andrews et al., 2002). As a result, a disturbance resulting in 67% mortality of sponges or corals would require 20–34 years for these organisms to recover 80% of their predisturbance biomass (Rooper et al., 2011). Their ecological importance, their vulnerability to damage or removal due to human activities, and their prolonged postdisturbance recovery times have led to the designation of some areas of notable coral and sponge diversity in the Aleutian Islands as "habitat areas of particular concern" under the Magnuson-Stevens Act and to their subsequent closure to fishing (Hourigan, 2009). Gaining greater understanding of the role that biogenic structures play in the distribution and abundance patterns of Pacific ocean perch in the broader context of the oceanographic habitats where they co-occur could prove valuable to

[1] Spencer, P. D., and J. N. Ianelli. 2010. Assessment of Pacific ocean perch in the Bering Sea/Aleutian Islands. *In* Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Islands Regions, p. 1033–1083. [Available from North Pacific Fishery Management Council, 605 West 4th Ave., Suite 306, Anchorage, AK 99510.]

[2] Reuter, R. 2015. Personal commun. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle, WA 98115.

the ecosystem-based management of this commercially harvested fish.

The primary objective of this study was to describe the distribution and abundance of Pacific ocean perch in relation to physical and biological oceanographic factors across this species' range, on the basis of data from bottom trawl surveys conducted periodically in the Aleutian Islands during the summer. We postulate that biogenic structures (sponges, corals, and bryozoans) can modify Pacific ocean perch distribution and abundance across gradients of environmental and physical conditions by providing additional structural heterogeneity in trawlable habitats where we sample. We used generalized additive modeling (GAM) to identify the physical and biological oceanographic predictor variables that influence the relationships between Pacific ocean perch distribution and abundance. We used field observations and out-group comparisons to validate the resulting models.

Materials and methods

Trawling procedures

A stratified-random sampling design was used for the AFSC RACE Division Aleutian Islands bottom trawl survey of trawlable areas shallower than the depth of 500 m across the Aleutian archipelago (Fig. 1). The survey area extends on the north side of the Aleutian island chain from Unimak Pass in the east (165°W) to Stalemate Bank in the west (170°E); on the south side of this archipelago, the survey extends from Samalga Pass (170°E) to Stalemate Bank in the west. Strata are based on 4 depth intervals (1–100 m, 101–200 m, 201–300 m, and 301–500 m) over the continental shelf and upper slope. The depth strata are further segregated by the North Pacific Fisheries Management Council's (NPFMC) Bering Sea Aleutian Islands regulatory area (NPFMC[3]) into survey districts that correspond to the NPFMC subdivisions of western, central, and eastern Aleutian districts and an additional southern Bering Sea survey district that roughly corresponds to the Bogoslof district. Trawl sample allocation in each stratum was achieved with a modified Neyman optimum allocation sampling strategy (Cochran, 1977) to provide representative samples of fishes and invertebrates occurring at each sampling location within each stratum.

Bottom trawl surveys were conducted according to standard protocols established in Stauffer (2004). Our goal was to land each trawl net quickly on the bottom in fishing configuration at a towing velocity of 1.5 m/s (3 kn) and to maintain vessel speed, with the net retaining fishing configuration and proper bottom contact for 15 min (an area of approximately 2.25 ha was swept on average during each tow). Tables of standard scope ratios of trawl warp in relation to bottom depth were used to reduce potential fishing power differences between the vessels used in different surveys. Date, time, and GPS-generated position were recorded throughout each tow; depth, water temperature, and time of collection also were recorded during each tow with an SBE 39[4] microbathythermograph (Sea-Bird Electronics, Inc., Bellevue, WA). During each tow, the vertical and horizontal trawl openings were measured with Scanmar acoustic net mensuration sensors (Scanmar International, Point Richmond, CA). A bottom contact sensor was attached to the midpoint of the roller gear and was used to measure the degree of contact between the ground gear and the bottom. Trawl hauls were performed during daylight hours (i.e., between 0.5 h after sunrise and 0.5 h before sunset), and all trawl performance data were judged after completion through the use of computer-generated graphics and data summaries. For our analyses, we included only catches obtained with satisfactory trawl net performance and bottom contact and only those for which distance fished, net width, bottom depth, and water temperature were recorded.

Data used to parameterize and select the best-fitting GAMs were collected during the periodic bottom trawl surveys of the Aleutian Islands used to assess Pacific ocean perch distribution and abundance. The survey completed in 2000 was the last in a series of triennial surveys. Since 2000, Aleutian Islands bottom trawl surveys have been conducted biennially with the exception of 2008, when insufficient funds led to the cancellation of that year's survey effort. For the surveys undertaken between 1997 and 2010, an average of 394 stations that met our criteria to be included in this study were sampled per year. Total station counts ranged from 355 in 2006 to 413 in 2002.

Physical variables

An array of physical, environmental, and spatial predictor variables was used to parameterize the GAMs. At each bottom trawl survey station, start and end positions of the trawl were recorded and bottom depth and temperature were measured. Kriging, a geostatistical procedure that estimates a spatial surface from an array of point values, was used to calculate an index of local bottom slope at each survey station from 100-m bathymetric contour increments between 0 and 2000 m derived from ETOPO2 gridded elevation data by following the method of Rooper and Martin (2009). Tide velocity (V_T) was predicted at each sampling station for the date and time of the bottom trawl survey by using tidal prediction software developed at Oregon State University (Tidal Prediction Software [OTPS], website accessed January 2010) (Egbert et al., 1994; Egbert

[3] NPFMC (North Pacific Fishery Management Council). 2014. Fishery management plan for groundfish of the Bering Sea and Aleutian Islands Management Area, 144 p. NPFMC, Anchorage, AK [Available at website.]

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

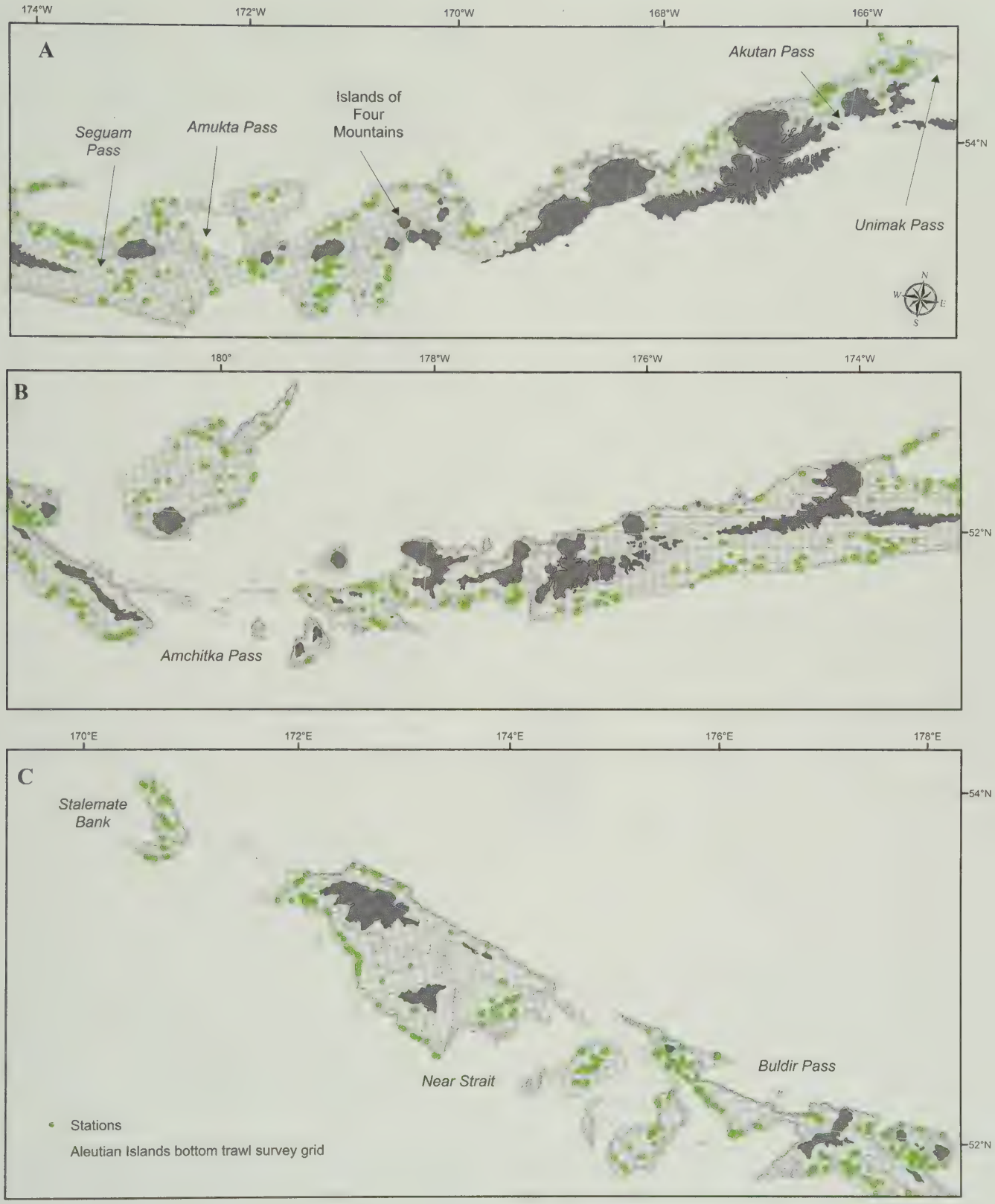

Figure 1

Map of the survey grid and trawl stations of the Alaska Fisheries Science Center Resource Assessment and Conservation Engineering Division Aleutian Islands bottom trawl survey sampled during 1997–2010 in the (**A**) eastern, (**B**) central, and (**C**) western Aleutian Islands.

and Erofeeva, 2002). To address current-dependent catchability of the bottom trawl, predicted tidal velocity was decomposed into component vectors with velocities parallel or perpendicular to the ship's direction of travel. The difference between the ship's bearing and the direction of tidal flow (Δ_θ) was calculated as

$$\Delta_\theta \sim if(\theta_T - \theta_S + 360° < 360°, \quad then(\theta_T - \theta_S + 360°), \quad else(\theta_T - \theta_S), \tag{1}$$

where θ_T = the direction of tidal flow; and
θ_S = the direction of the ship's travel during the trawl survey.

Parallel current (C_P) was then calculated as

$$C_P \sim if(90° < \Delta_\theta < 270°, \quad then\left(-\sqrt{\frac{v_T^2}{1+\left(tan(\Delta_{\theta(r)})\right)^2}}\right), \quad else\sqrt{\frac{v_T^2}{1+\left(tan(\Delta_{\theta(r)})\right)^2}}, \tag{2}$$

where $\Delta_{\theta(r)}$ = the angular difference between the direction of tide flow and ship's travel.

Note that C_p carries a negative sign if it is opposite the ship's direction of travel. Because the speed of water flowing through the mouth of the trawl is an important factor that could affect the catch efficiency of the bottom trawl, we estimated trawl velocity at the net mouth (N_S) as

$$N_S \sim v_S - C_p, \tag{3}$$

where v_S = the ship's velocity.

Finally, cross current (C_x) can be estimated as

$$C_x \sim C_p tan(\Delta_{\theta(r)}). \tag{4}$$

Its absolute value ($|C_x|$) was included in the model.

Invertebrate data

The precision of sponge identification by scientists during the Aleutian Islands bottom trawl surveys has varied over time and remains challenging (Stone et al., 2011). We chose to examine the Aleutian Islands surveys between 1997 and 2010 because, with the advent of waterproof invertebrate field guides for use on deck in 1996 (Kessler[5]), 1997 (Clark[6]), 1999 (Clark[7]), and 2006 (Clark[8]), our ability to consistently identify sponges and other invertebrates to higher taxonomic levels in the field was enhanced. As AFSC field biologists have become more familiar with these identification tools, the number of sponge taxa reported from the Aleutian Islands bottom trawl survey has also increased, rising from 7 in 1994 to around 70 in 2006 and 2010. Recently, Stone et al. (2011) recognized 125 unique sponge taxa from the Central Aleutian Islands and indicated that there were likely many more species yet to be described from this region.

Sponges were identified on Aleutian Islands bottom trawl surveys to the lowest possible taxonomic level on the basis of the existing field guides, but identifications depended on the identifier's expertise as well as on the minimum level of identification required that year, both of which varied within and between survey years. The uncertainty in our taxonomic identifications of sponges coupled with our primary aim of considering their contribution to structural heterogeneity in the environment led us to employ Bell and Barnes' (2000) method of grouping sponges by body form into morphological groups (i.e., morphogroups). By combining this technique with a modified version of the list of macroscopical features in Boury-Esnault and Rützler's (1997) thesaurus of sponge morphology, we created 15 morphogroups representing local Aleutian sponge fauna (Fig. 2) and assigned field identified sponges to these groups ex post facto. A group composed of identifiable sponges that did not fit into 1 of the 15 morphogroups (e.g., *Plakina tanaga*) and unidentifiable fragments of sponges were assigned to a general category entitled "Porifera unidentified."

Corals and bryozoans are epibenthic invertebrates that also provide biogenic structure, which may serve as habitat resources for Pacific ocean perch in this part of their range (Rooper and Boldt, 2005; Rooper et al., 2007; Boldt and Rooper, 2009). To allow comparison with these and similar studies (e.g., Rooper and Martin, 2012), we grouped the coral and bryozoan taxa into single presence–absence composite "corals" and "bryozoans" factors, respectively. Wing and Barnard (2004) included 105 coral species from Alaska waters in their revised field guide. Heifetz et al. (2005) documented 69 taxa of corals in the Aleutian Islands; 25 of them were endemic to the region. For this study, the composite corals factor was composed of members of the orders Alcyonacea, Anthoathecata, Antipatharia, and Scleractinia. From these orders, 99 unique taxa were reported from our catches during the Aleutian Islands bottom trawl surveys conducted between 1997 and 2010. The

[5] Kessler, D. W. 1996. Alaska's saltwater fishes and other sea life. Unpubl. manuscript. Revision by staff of the Alaska Fish. Sci. Cent. Resource Assessment and Conservation Engineering (RACE) Division (for use at sea) of Kessler, D. W. 1985. Alaska's saltwater fishes and other sea life, 358 p. Alaska Northwest Publishing Co., Anchorage, AK.

[6] Clark, R. N. 1997. Invertebrates of the Aleutian Islands, 169 p. Unpubl. manuscript. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

[7] Clark , R. N. 1999. Gulf of Alaska invertebrates, 100–1000 m, 179 p. Unpubl. manuscript. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

[8] Clark, R. N. 2006. Field guide to the benthic marine invertebrates of Alaska's shelf and upper slope taken by NOAA/NMFS/AFSC/RACE Division trawl surveys, 305 p. Unpubl. manuscript. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

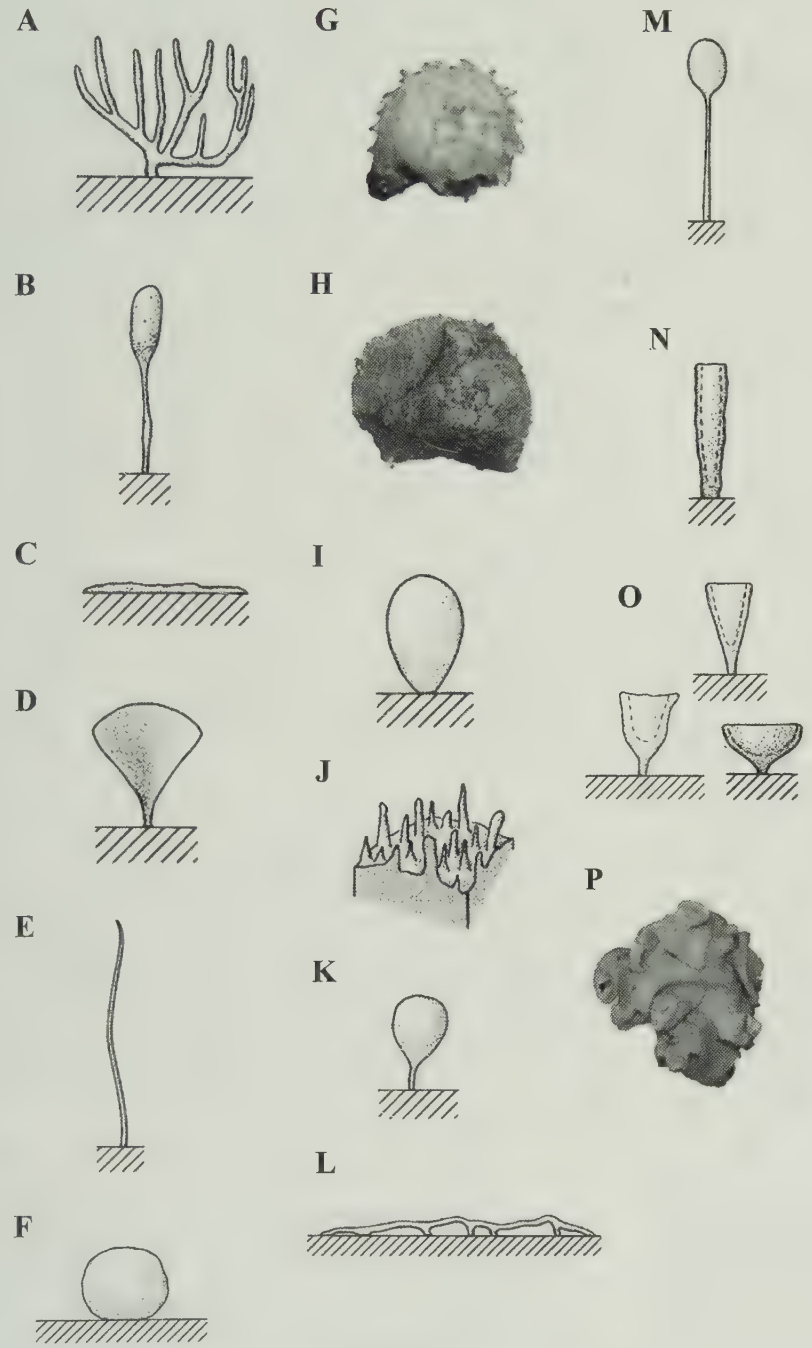

Figure 2

Nominal morphogroups assigned to field identified sponges on the basis of morphotypes from Boury-Esnault and Rützler (1997) and Bell and Barnes (2000): (**A**) arborescent, (**B**) clavate, (**C**) encrusting, (**D**) flabellate, (**E**) flagelliform, (**F**) globular, (**G**) globular-papillate (e.g., *Weberella bursa*, an image of which represents this morphogroup in this figure), (**H**) massive (e.g., *Halichondria* spp.), (**I**) ovate, (**J**) papillate, (**K**) pedunculate, (**L**) repent, (**M**) stipitate, (**N**) tubular, and (**O**) vase. (**P**) The Porifera unidentified group is represented by an identifiable sponge (e.g., *Plakina tanaga*) that did not fit in to the predetermined morphogroups. Globular-papillate and vase morphogroups are modified from those of Boury-Esnault and Rützler (1997) to incorporate local faunal variants; for example, the vase morphogroup is a composite of the turbinate, caliculate, and infundibuliform morphotypes from Boury-Esnault and Rützler (1997).

majority of these taxa (85) are primnoids, gorgonians, stony corals, and octocorals, all of which provide vertical relief over the trawlable habitats we sampled, and a few are among the tallest biogenic structures that occur in the Aleutian Islands (e.g., *Primnoa willeyi* can reach 3 m in height). Similarly, we included all bryozoans reported from our Aleutian Islands bottom trawl catches (~25 taxa) as a composite predictor variable because of the biogenic structure they may provide.

Our standard trawl net with its rubber bobbin roller gear (Stauffer, 2004) is not optimized for collecting attached epibenthic invertebrates. Therefore, all of the biogenic structures used to parameterize our models were coded as presence or absence before analyses. We also considered that trawl nets sampled sponges differentially (see Wassenberg et al., 2002), integrating their actual distribution over trawlable bottom for the duration of the trawl haul. Therefore, we consider the coding of biogenic structures in our trawl catches as presence–absence factors to be a conservative measure of their occurrence.

Fish data

Catch per unit of effort (CPUE) was measured in kilograms per hectare and calculated for juvenile and adult Pacific ocean perch with the area-swept method (Wakabayashi et al., 1985). Length composition, estimated for each trawl by measuring a selected subset of up to 200 fork lengths (FL) of Pacific ocean perch from the catch, was used to proportionally allocate the catch of Pacific ocean perch on the basis of length at first maturity (Paraketsov, 1963; Chikuni, 1975) into juveniles (FL≤250 mm) and adults (FL>250 mm) for each trawl tow. Nonzero CPUE values (conditional abundance) were log-transformed and then placed on a common propor-

Table 1

Independent variables that parameterized the generalized additive models used to predict presence, absence, and abundance of Pacific ocean perch (*Sebastes alutus*). Sponge morphogroups were coded as presence-absence factors (1 or 0, respectively), and the units for continuous variables are temperature (°C), depth (m), local slope (°), and for velocity measures (cm/s). Note that Sp is a composite term substituted for all sponge morphogroups and U during model formulation.

Factors	Continuous variables
A=arborescent	T=temperature
C=clavate	D=depth
E=encrusting	Sl=local slope
F=flabellate	Long.=longitude
Fl=flagelliform	C_x=cross current
G=globular	N_S=trawl velocity
Gp =globular-papillate	V_T=tide velocity
M=massive	
O=ovate	
P=papillate	
Pe=pedunculate	
R=repent	
S=stipitate	
Tu=tubular	
V=vase	
U=Porifera unidentified	
Sp=all sponges, composite	
Co=all corals, composite	
Br=all bryozoans, composite	

tional scale by dividing individual CPUE estimates by the sum of the annual CPUE within each cruise year; by design, this approach ignored interannual differences in Pacific ocean perch abundance in favor of allowing interannual comparisons during model validation.

Modeling

Pacific ocean perch distribution and abundance were modeled with the nonparametric regression technique of GAMs (Hastie and Tibshirani, 1986) in R statistical software, vers. 2.13.1 (R Core Development Team, 2011) and the mgcv package (Wood, 2006). This fish species is patchily distributed across our survey area and, typical of field collected data, presents a greater proportion of zero catches than would be expected from a Poisson distribution, resulting in abundance data that are overdispersed (McCullagh and Nelder, 1989). To model these zero-inflated catch data, we followed the recommendation of Barry and Welsh (2002) and undertook independent GAM selection for the Pacific ocean perch presence–absence and conditional abundance data sets. The presence–absence GAMs used a binomial distribution with a logit link function; the conditional abundance models employed a Gaussian distribution with an identity link function.

Probability of presence and conditional abundance of Pacific ocean perch was predicted from GAMs parameterized with a variety of physical, environmental, spatial, and biogenic variables (for a list of these variables and their abbreviations, see Table 1). To reduce the tendency of GAMs to over-fit data, we constrained the degrees of freedom (df) for some of the smoothed continuous terms in the models (i.e., df=4 for local slope [Sl], V_T, C_x, and N_s; df=10 for depth and temperature combined [D,T]). To identify interdependencies amongst continuous predictor variables we examined Pearson's correlation coefficient (r; Krebs, 1989) for all pairwise comparisons and determined that only depth and temperature were moderately correlated ($|r|=0.55$). Consequently, we combined depth and temperature into a bivariate interaction term in the GAM. To determine interdependency of sponge morph, bryozoan, and coral presence–absence factors, we computed Pearson's coefficient of mean square contingency (Φ; Zar, 1984), found that for all pairwise comparisons $|\Phi|$ was <0.50, and consequently included each biogenic presence–absence factor as an independent predictor in the GAM.

Four candidate models for the prediction of presence or conditional abundance of juvenile and adult Pacific ocean perch underwent backward stepwise term selection (Weinberg and Kotwicki, 2008; Zuur et al., 2009). The 4 initial model formulations for both of those response variables were

$$\sim A + C + E + F + Fl + G + Gp + M + O + Pe + R + S + Tu + V + U + Co + Br + s(Long.) + s(Sl) + s(N_S) + s(C_x) + s(D,T), \quad (1)$$

$$\sim A + C + E + F + Fl + G + Gp + M + O + P + Pe + R + S + Tu + V + U + Co + Br + s(Long.) + s(Sl) + s(V_T) + s(D,T), \quad (2)$$

$$\sim Sp + Co + Br + s(Long.) + s(Sl) + s(N_S) + s(C_x) + s(D,T), \quad (3)$$

$$\sim Sp + Co + Br + s(Long.) + s(Sl) + s(V_T) + s(D,T). \quad (4)$$

Formulations 1 and 2 contained the full suite of 18 presence–absence factors for biogenic structures (15 sponge morphogroups [for abbreviations of these factors, see Table 1] and 1 term each for Porifera unidentified [U], all corals, composite [Co], and all bryozoans, composite [Br]) as well as the smooth terms longitude (Long.), Sl, and D,T. These model formulations differed by using either (1) the 2 smoothed vector components of V_T (C_x and N_S) or 2) simply smoothed V_T. Formulations 3 and 4 used a reduced predictor variable set by combining all sponges into a single presence–absence term (Sp) and then testing both suites of smooth terms as applied in formulations 1 and 2. Backward stepwise term selection involved fitting each of the 4 formulations above independently with a GAM and then removing the least significant terms iteratively until only significant predictor terms remained. Significance for all models and statistical tests was inferred

from $P<0.05$. The best-fitting GAMs among the 4 starting models that predicted juvenile or adult presence or abundance were selected on the basis of the lowest Akaike's information criterion scores.

Predicted presence of juvenile and adult Pacific ocean perch, based on the GAMs formulated with data from the period 1997–2010, was validated by comparison with observed presence of this species from the 2012 Aleutian Islands bottom trawl survey. Comparisons were made with Cohen's kappa coefficient (k; Manel et al., 2001), which measures the proportion of correctly predicted cases of presence or absence after accounting for chance effects. This coefficient ranges from 0 to 1, corresponding with poor to near perfect agreement (Landis and Koch, 1977).

For conditional CPUE models, we used a form of jack-knifing, iteratively leaving out a single year of data, to internally validate the GAM. Residual deviance from each iteration of this cross-validation was used to compute a pseudocoefficient of determination (r^2; O'Brien and Rago, 1996) that was used to measure model fit. The residual deviance (RD) is the deviance remaining in the data that is unexplained by the full model (i.e., RD=1–r^2). By iteratively dropping terms retained in the best-fitting GAM and recalculating r^2, we were able to assess the relative contribution of that term to the deviance explained by the model, thereby estimating its leverage in the GAM.

Table 2

Prevalence of biogenic structures, measured as percent frequency of occurrence in trawl tows per annum, in catches of bottom trawl surveys conducted in the Aleutian Islands between 1997 and 2010.

	Survey year					
Substratum	1997	2000	2002	2004	2006	2010
Porifera unidentified	63	78	74	78	78	77
Corals	48	51	52	49	50	55
Globular-papillate	43	52	47	46	43	55
Globular	43	39	44	39	37	36
Flabellate	35	37	39	34	34	47
Arborescent	27	41	34	25	32	35
Massive	29	30	25	28	33	38
Papillate	21	30	24	24	37	28
Bryozoans	23	32	14	15	13	24
Vase	12	14	16	18	14	20
Ovate	10	4	10	13	6	14
Repent	0	0	0	4	7	10
Tubular	0	0	2	4	3	4
Encrusting	0	2	2	4	0	2
Clavate	1	2	1	0	2	0
Flagelliform	0	0	1	1	1	0
Stipitate	0	0	0	0	2	1
Pedunculate	<1	0	<1	0	0	0

Results

Summary of biological collections

Between 1997 and 2010, 6 summer bottom trawl surveys were conducted in the Aleutian Islands by AFSC, resulting in a total of 2364 stations included in this study. The Pacific ocean perch was consistently ranked amongst the most abundant fish species collected on these surveys and commonly occurred in the survey catches; they were caught in 58% of the standard survey tows. Of the trawl catches, 23% contained juvenile Pacific ocean perch and 53% contained adults. Juveniles co-occurred with adults in about one-third of the trawl catches (34%), and the majority of trawl catches with juveniles also contained adults (79%). Sponges and corals were common in hauls of the Aleutian Islands bottom trawl surveys as well; they occurred in about 87% of the trawl catches.

Sponges were the most commonly occurring structure-forming invertebrate collected in our surveys between 1997 and 2010, followed by corals and bryozoans. The majority of the trawl tows selected for analyses contained sponges and corals, which were also present in most of the catches containing Pacific ocean perch (about 91%). The composite corals group occurred in just over half (51%) of the tows in all survey years. Of catches containing juvenile Pacific ocean perch, 96% also collected sponges or corals, but the rate of co-occurrence for adults was lower (90%). Bryozoans were less common in our catches than were sponges or corals, occurring, on average, in about 20% of the trawl hauls. They were also less common in hauls that contained Pacific ocean perch juveniles or adults, occurring in about 20% of these hauls.

"Porifera unidentified" was the most common sponge category occurring in our survey tows each year (Table 2). Globular (G) and globular-papillate (Gp) sponges occur at similar or slightly elevated rates compared with some of the larger morphotypes (e.g., arborescent [A], flabellate [F], and massive [M]). Clavate (C), encrusting (E), and tubular (Tu) sponges were less common, and pedunculate (Pe) sponges were the rarest morphotype collected.

Summary of environmental and physical data

Bottom trawl hauls included in this study were conducted over a wide variety of physical and oceanographic conditions. The deepest trawl hauls during the study period were conducted at 488 m and the shallowest at

Table 3

Backward stepwise term selection used in identification of the best-fitting generalized additive models (GAM) for predicting distribution and abundance of Pacific ocean perch (*Sebastes alutus*) on the basis of data from bottom trawl surveys conducted in the Aleutian Islands during 1997–2010, including the percent contribution of each predictor variable to the deviance explained by the best-fitting model and Akaike's information criterion score (AIC). An asterisk (*) indicates the best-fitting GAM formulation. See *Materials and methods* section for initial model formulations and Table 1 for definitions of variable abbreviations. CPUE=catch per unit of effort.

Life stage	Response variable	Initial model formulation	Independent variables retained	Contribution by each variable (%)	Deviance explained (%)	AIC
Juvenile	Presence–absence factor	1	$F+G+Gp+M+U+Co+Br+s(Log.n)+s(Sl)+s(D,T)+s(C_x)$		24.9	1971.77
		2	$F+G+Gp+M+U+Co+Br+s(Long.)+s(Sl)+s(D,T)+s(V_T)$	2.7;3.1;0.9;0.6;3.0;1.0; 1.1; 12.3;2.1;40.9;1.7	25.0	1970.10*
		3	$Sp+Co+s(Long.)+s(Sl)+s(D,T)+s(C_x)$		20.7	2070.22
		4	$Sp+Co+s(Long.)+s(Sl)+s(D,T)+s(V_T)$		20.9	2068.65
Juvenile	Conditional CPUE	1 and 2	$C+O+V+s(Log.n)+s(D,T)$	3.3;5.5;4.3;41.7;26.8	24.9	2358.05*
		3 and 4	$s(Long.)+s(D,T)$		22.0	2372.99
Adult	Presence–absence factor	1	$F+G+U+Br+s(Long.)+s(Sl)+s(D,T)+s(N_s)$		38.6	2054.45
		2	$F+G+U+Br+s(Long.)+s(Sl)+s(D,T)+s(V_T)$	1.4;0.4;0.8;0.9;6.6;1.8; 68.8;0.9	38.7	2050.85*
		3	$Sp+Co+Br+s(Long.)+s(Sl)+s(D,T)$		37.7	2079.74
		4	$Sp+Co+Br+s(Long.)+s(Sl)+s(D,T)+s(V_T)$		38.0	2073.70
Adult	Conditional CPUE	1 and 2	$G+Co+s(Long.)+s(Sl)+s(D,T)$	1.4;0.7;14.2;1.4;84.0	42.5	5692.83*
		3 and 4	$Br+s(Lon)+s(Sl)+s(D,T)$		42.0	5702.49

32 m. Many of the deeper stations are near passes between islands in the Aleutian archipelago, but, in general, deeper stations occur more frequently in the eastern part of the survey area (around Samalga, Amukta, and Seguam passes) than in the west. The values for Sl from the kriged bathymetry at trawl stations ranged from 0° to 15°. Tidal currents predicted at each bottom trawl haul from the tidal prediction model ranged from <1 cm/s to ~ 300 cm/s (around 3 m/s or 6 kn). The highest current velocities were predicted around Seguam and Amukta passes, and some additional areas of high current were predicted on the east side of Amchitka Pass. Bottom temperatures (T) measured in situ during trawl hauls ranged from 3°C to 7°C.

Results of generalized additive modeling

Prediction of presence and absence The best-fitting GAMs for predicting the probability of presence of juvenile and adult Pacific ocean perch in the Aleutian Islands accounted for a quarter of the deviance in the juvenile model and 38.7% of the deviance in the adult model (Table 3). The depth distribution of adults, centered around 225 m, was deeper than that of juveniles, found at depths around 150 m. Model effects showed very little dependence on temperature (Figs. 3 and 4). Model responses (GAM effects represented by the solid lines on graphs) indicate increased probability of encountering Pacific ocean perch life stages when >0 and decreased probability when <0. The standard error generally increases around the predictions for which sample size decreases, signifying areas of lower confidence in the model. Geographically, the predicted odds of collecting either life stage increased at Unimak Pass (165°W), in the passes near the Islands of Four Mountains (170°W), in Amukta and Buldir passes (173°W and 177°E), and in Near Strait (175°E; Figs. 5 and 6). Effects due to local slope were similar for both juveniles and adults and the probabilities of encountering either life stage increased over moderate slopes up to around 5° of incline.

Increasing tidal velocities initially led to increased probability of encountering adults, but the probability of encounter for juveniles steadily decreased with increasing velocities. The presence of biogenic structures accounted for more of the deviance explained in the juvenile presence–absence model than with the adult model (11.3% versus 2.6%; Table 3). The biogenic struc-

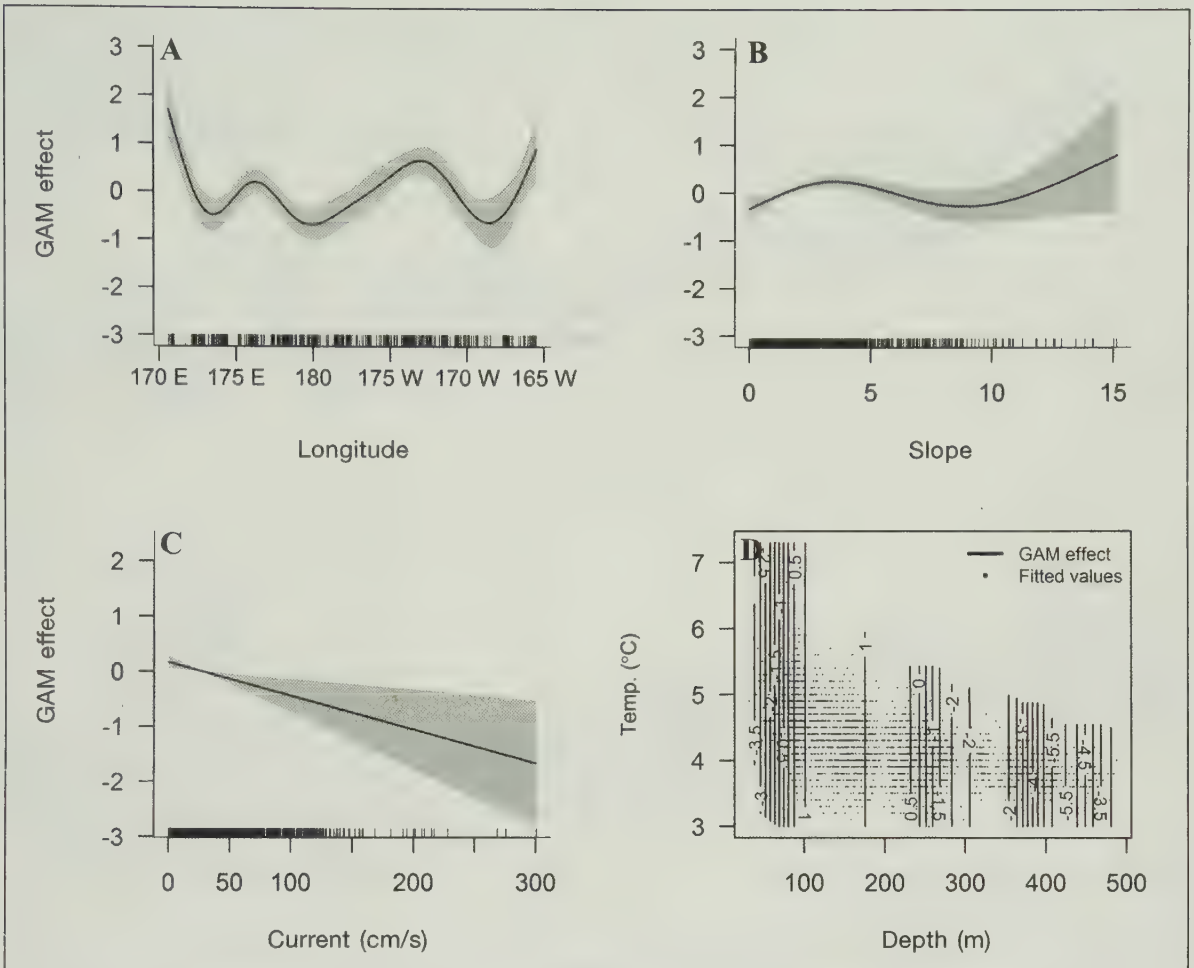

Figure 3

From the best-fitting generalized additive model (GAM), predictions of presence of juvenile Pacific ocean perch (*Sebastes alutus*) at trawl stations in the Aleutian Islands during 1997–2010 in relation to (**A**) longitude, (**B**) kriged bottom slope, (**C**) predicted tidal current velocity, and (**D**) the interaction between depth and temperature. A change in number orientation indicates that either a maximum or a minimum was reached for the GAM effect.

tures retained in the models were either erect forms (e.g., F or Co) or have been reported to be epizoic on erect sponges (e.g., G and Gp sponges; Stone et al., 2011). Although the presence of certain sponge morphogroups and Co was associated with increasing probability of encountering juveniles and adults, the presence of Br was associated with decreasing probability of encountering either life stage of Pacific ocean perch. This decrease may result from the shallower depth distribution of Br (depths <110 m) compared with the depth distribution of Pacific ocean perch juveniles (depths ~150 m) and adults (depths ~225 m). More than half of the deviance explained in each presence-absence GAM was attributable to the D,T and Long. terms.

Validation of presence–absence generalized additive modeling The success of the GAMs to predict Pacific ocean perch distribution (presence) varied with life stage (Figs. 5 and 6). Based on the scale proposed by Landis and Koch (1977) for assessing model performance, the GAM predictions of presence of juvenile Pacific ocean perch from 2012 survey data displayed moderate agreement with trawl observations from the same year (k=0.52). GAM predictions of adult presence were more accurate, showing substantial agreement when predicted presence or absence of adults was compared with observed adult distribution for 2012 (k=0.70).

Prediction of conditional abundance More deviance in the model was explained by the best-fitting conditional abundance GAM for adults than by the best-fitting GAM for juveniles (Table 3). As with the presence–absence GAMs, the D,T and Long. terms were the most influential predictors of conditional abundance. Unlike the results from the presence–absence GAMs, there were temperature-related optima in both the juvenile

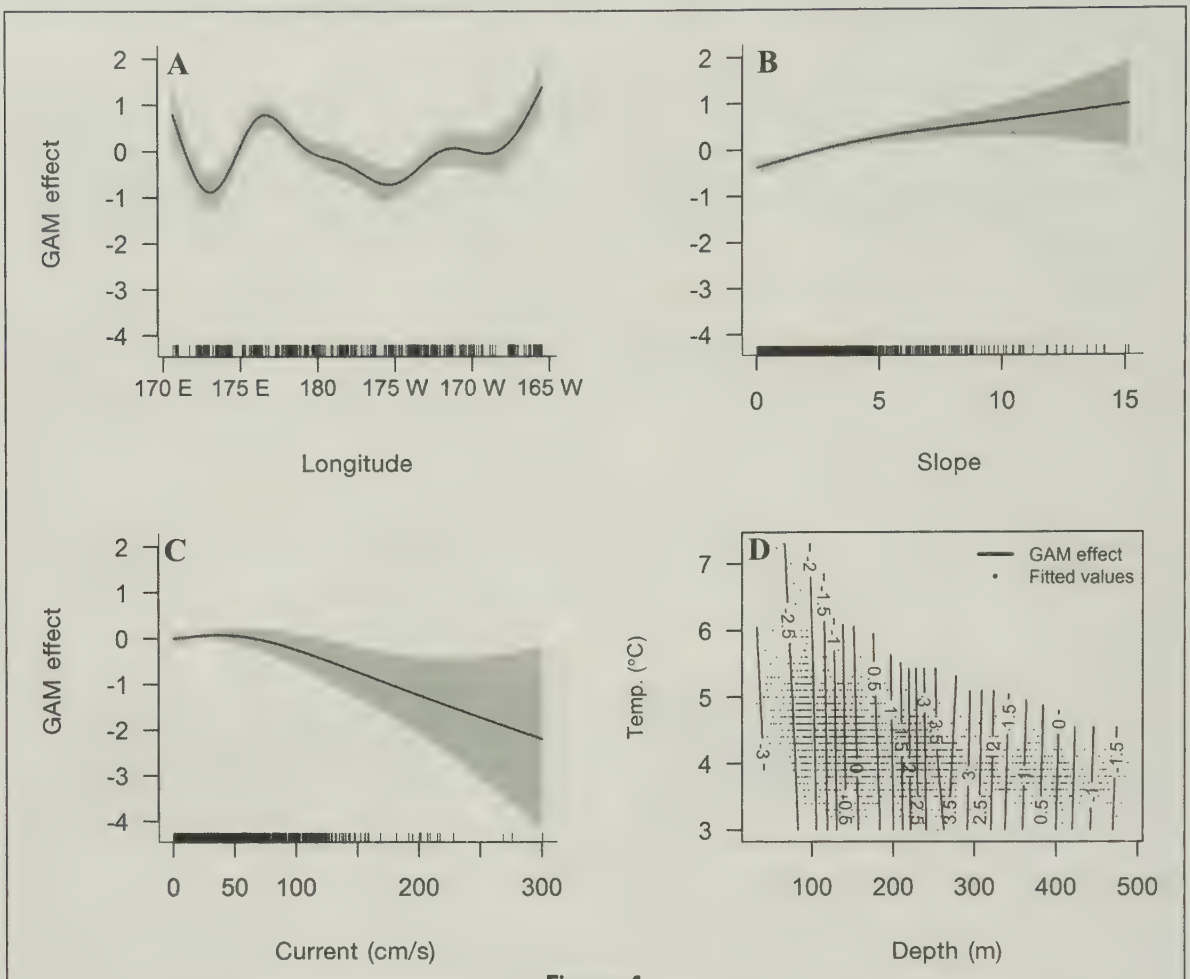

Figure 4

From the best-fitting generalized additive model (GAM), predictions of presence of adult Pacific ocean perch (*Sebastes alutus*) at trawl stations in the Aleutian Islands during 1997–2010 in relation to (**A**) longitude, (**B**) kriged bottom slope, (**C**) predicted tidal current velocity, and (**D**) the interaction between depth and temperature. A change in number orientation indicates that either a maximum or a minimum was reached for the GAM effect.

and adult conditional abundance GAMs (Figs. 7 and 8). Similar D,T-dependent optima were observed for juvenile and adult Pacific ocean perch abundance where present, and predicted conditional abundance was highest over depths of 200–250 m and a temperature range of 4.5–5.0°C. As with the predictions of increased probability of occurrence from the presence–absence GAMs, some of the highest predicted conditional abundances for either life stage are associated with major Aleutian passes. Higher abundances were predicted around Buldir Pass (176°E) and Seguam Pass (173°W), and some decreased abundances were predicted around the Islands of Four Mountains (170°W). Predicted adult conditional abundance increased with increasing Sl, up to an incline of around 5°, but Sl was not a predictor retained in the juvenile conditional abundance GAM.

Fewer biogenic structures were retained in the best-fitting conditional abundance GAMs, than in the presence–absence GAMs, but the relative contribution of these predictors to the deviance explained in the model was similar within each life stage (Table 3). The combined deviance explained by the presence or absence of biogenic structures remained a more important proportional contributor to the total deviance explained in the juvenile conditional abundance GAM than in the adult GAM (13.1% versus 2.1%). When sponges of the C and V morphogroups were present, the predicted juvenile conditional abundance was higher, but the presence of sponges of the ovate [O] morphogroup was associated with a decrease in the abundance of juveniles where present. For adults, conditional abundance increased in the presence of Co and decreased in the presence of sponges of the G morphogroup.

Validation of conditional abundance generalized additive modeling By cross-validating our GAM predictions it-

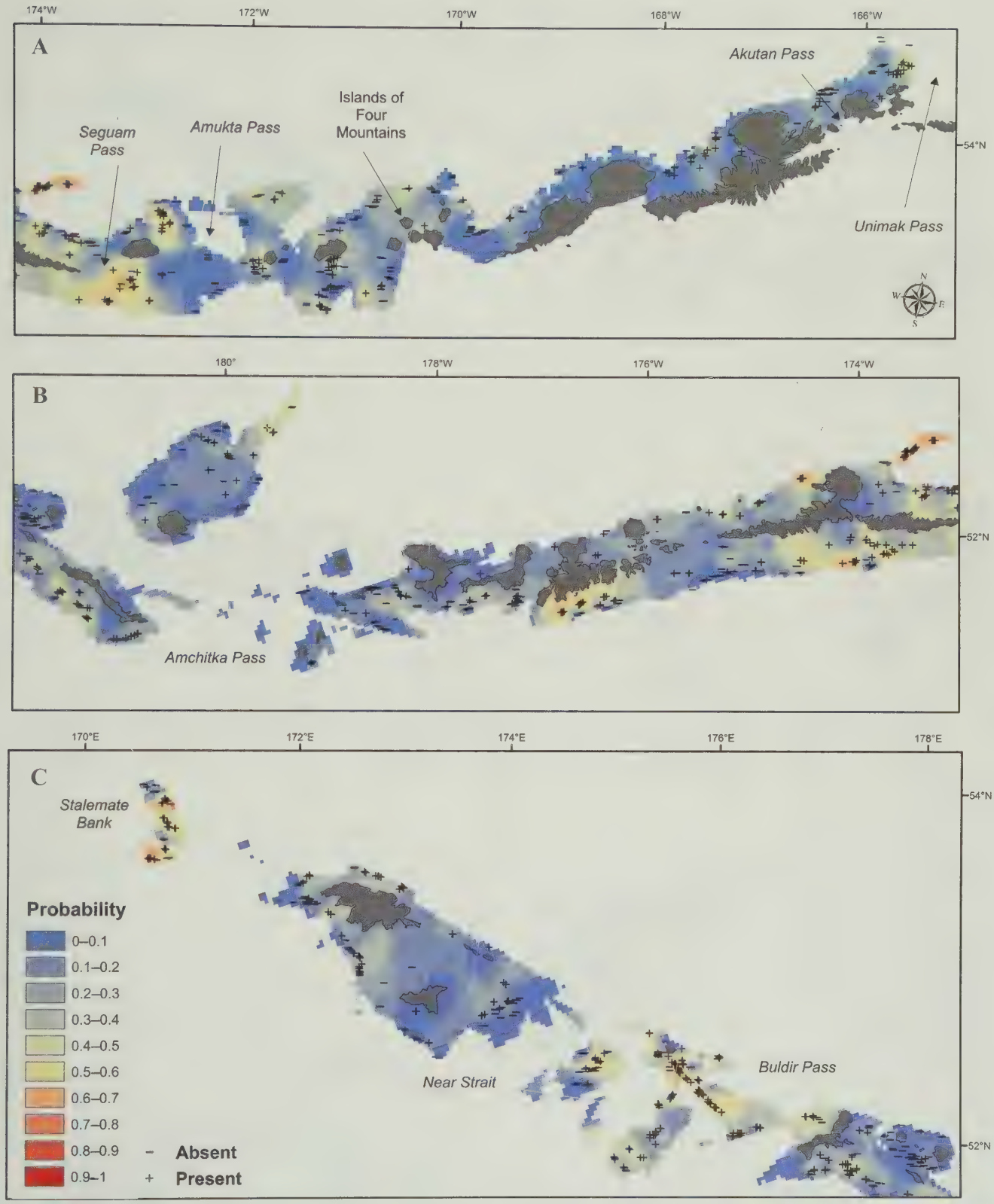

Figure 5

Observed (symbols) and predicted (shaded) presence or absence of juvenile Pacific ocean perch (*Sebastes alutus*) over an inverse distance-weighted surface from a generalized additive model based on Aleutian Islands bottom trawl surveys conducted during 1997–2010 across the (**A**) eastern, (**B**) central, and (**C**) western Aleutian Islands.

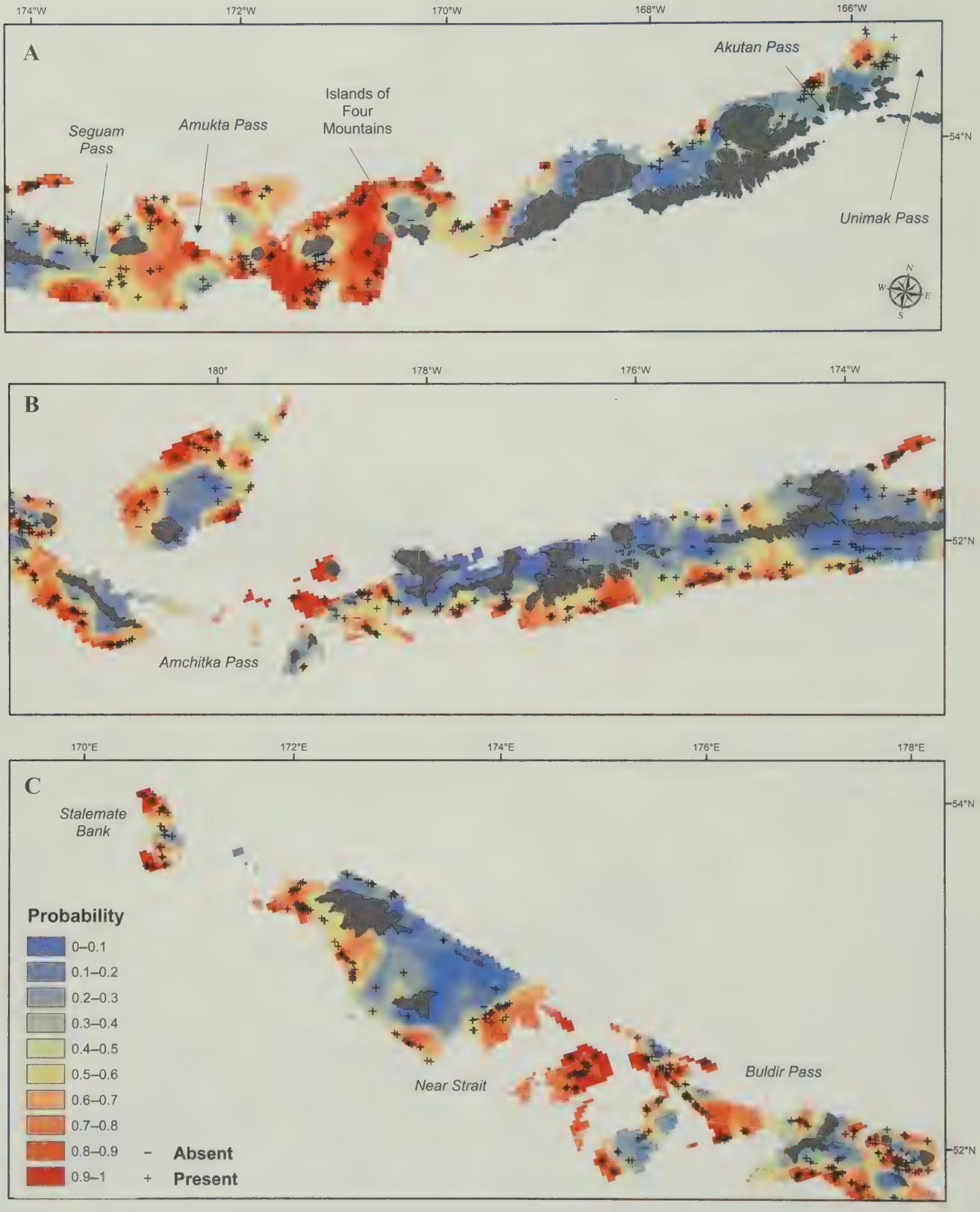

Figure 6

Observed (symbols) and predicted (shaded) presence or absence of adult Pacific ocean perch (*Sebastes alutus*) over an inverse distance-weighted surface from a generalized additive model based on Aleutian Islands bottom trawl surveys conducted during 1997–2010 across the (**A**) eastern, (**B**) central, and (**C**) western Aleutian Islands.

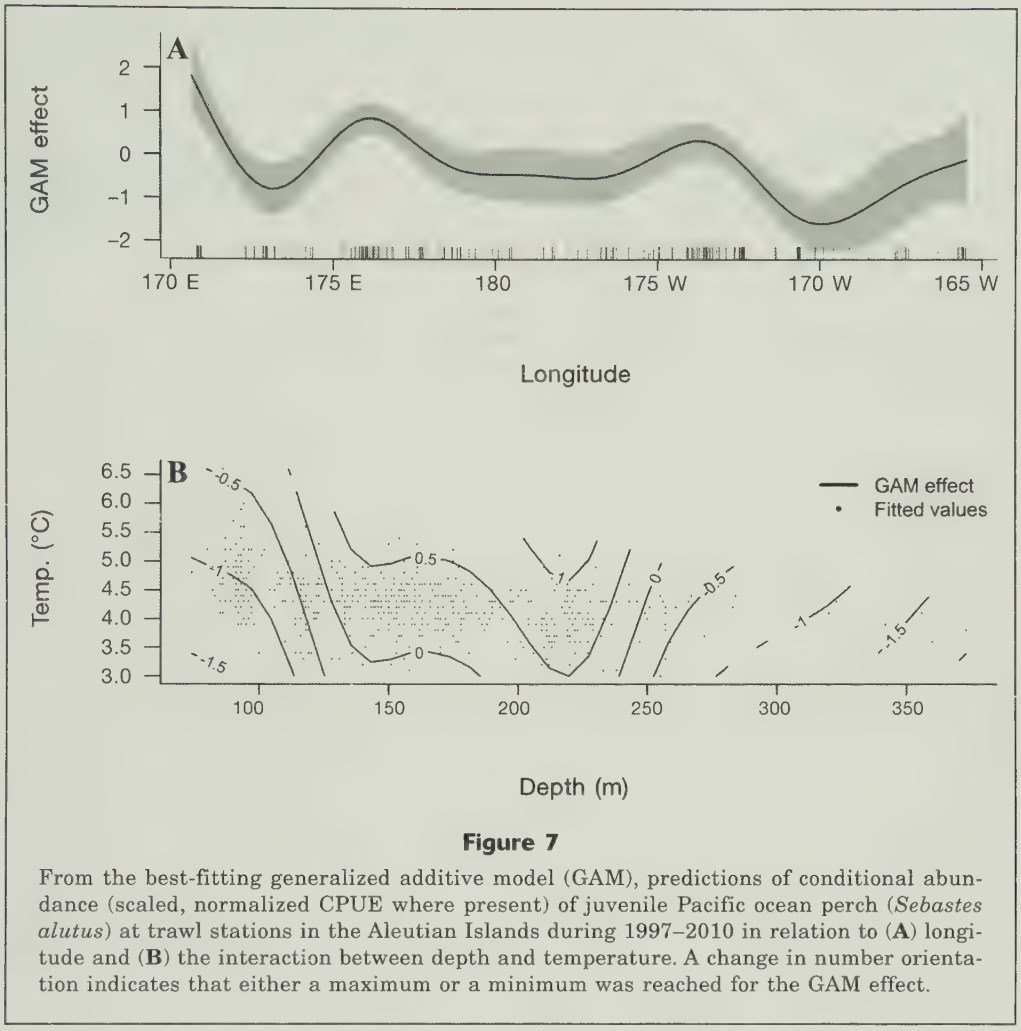

Figure 7

From the best-fitting generalized additive model (GAM), predictions of conditional abundance (scaled, normalized CPUE where present) of juvenile Pacific ocean perch (*Sebastes alutus*) at trawl stations in the Aleutian Islands during 1997–2010 in relation to (**A**) longitude and (**B**) the interaction between depth and temperature. A change in number orientation indicates that either a maximum or a minimum was reached for the GAM effect.

eratively against excluded years, we showed that the conditional abundance GAMs did a fair job of predicting juvenile Pacific ocean perch abundance and a better job for adults than for juveniles. The deviance explained in each of the jack-knifed cross-validations ranged from 23.2% to 28.5% for juveniles and from 41.4% to 44.8% for adults. Examination of diagnostic plots and residuals indicated that model assumptions were met.

Discussion

Depth, temperature, and proximity to major Aleutian passes (D,T and Long., respectively) were dominant influences in our GAMs (i.e., accounted for the greatest proportion of the deviance explained) and operated over broad spatial scales. These effects compared favorably with similar findings of other researchers by confirming the depth distributions and temperature affiliations of Pacific ocean perch life stages (Carlson and Haight, 1976; Brodeur, 2001; Love et al., 2002; Rooper and Boldt, 2005; Rooper 2008). The GAMs predicted increases of occurrence and abundance of Pacific ocean perch in proximity to most major Aleutian passes (e.g., Amukta, Seguam, and Buldir) that were similar to findings by Logerwell et al. (2005). We also determined that the inclusion of predictors that act over more local scales (e.g., biogenic structures and slope of the bottom at a sampling station) can improve the GAM fit and enhance our understanding of Pacific ocean perch distribution and abundance patterns within the context of broader scale oceanographic processes.

Logerwell et al. (2005) concluded that patterns of demersal fish distribution and abundance could reflect proximity to biological "hot spots," where prey aggregations form and productivity increases because of the convergence of bathymetric and hydrographic processes, such as those observed near Aleutian passes. There is substantial tidal mixing in the passes (Ladd et al., 2005), and the dominant flow of water through them is from the south to the north (Stabeno et al., 1999). The tidal mixing, the persistent northward water movement, and the interaction of mixed water with the euphotic zone near these passes often create local

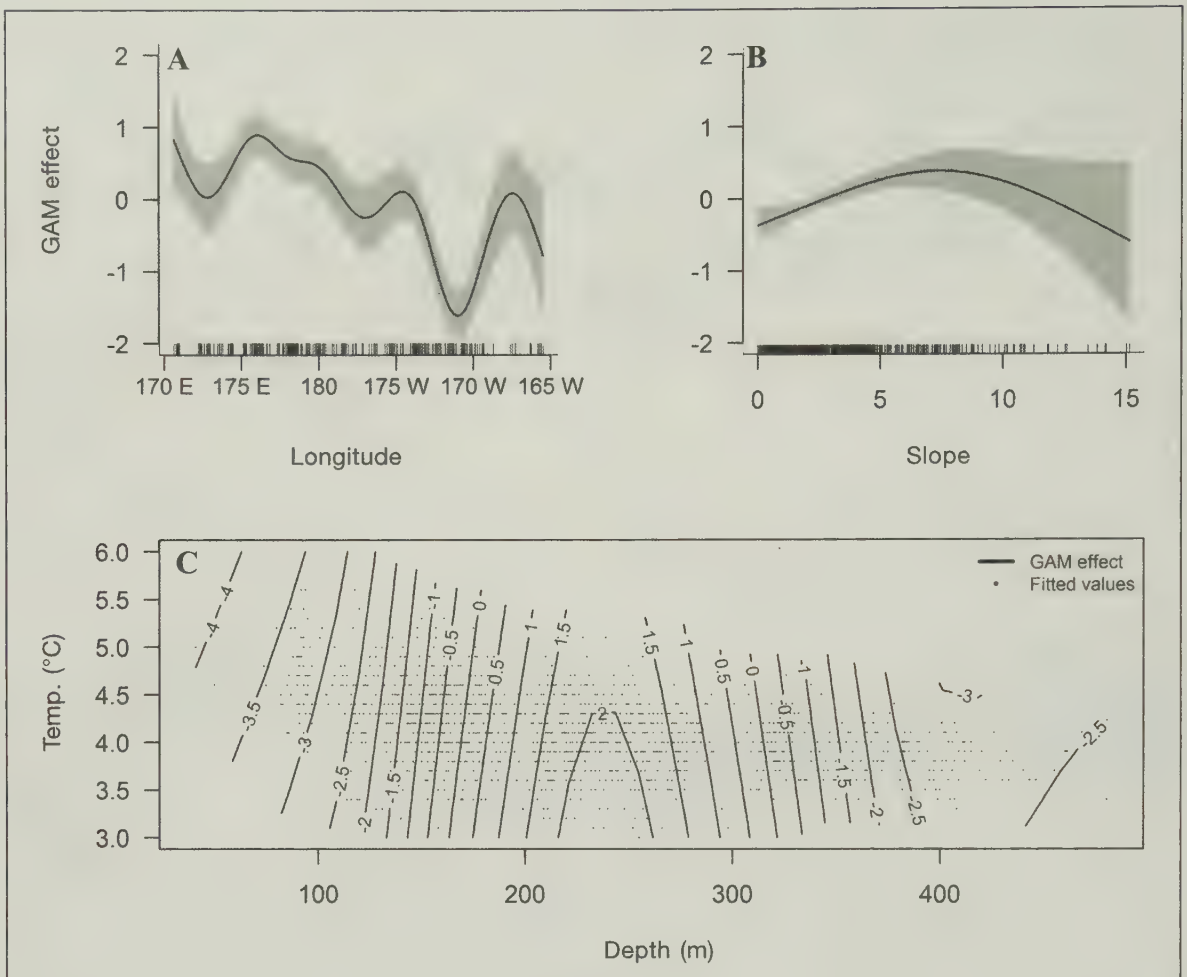

Figure 8

From the best-fitting generalized additive model (GAM), predictions of conditional abundance (scaled, normalized CPUE where present) of adult Pacific ocean perch (*Sebastes alutus*) at trawl stations in the Aleutian Islands during 1997–2010 in relation to (**A**) longitude, (**B**) kriged bottom slope, and (**C**) the interaction between depth and temperature. A change in number orientation indicates that either a maximum or a minimum was reached for the GAM effect.

regions of high production, especially to the north of the passes (Ladd et al., 2005). In addition, upwelling can occur around passes and may enhance local production (Swift and Aagaard, 1976; Coyle, 2005), leading to potentially greater abundance of the zooplankton prey of Pacific ocean perch (Carlson and Haight, 1976; Brodeur, 1983; Boldt and Rooper, 2009). Southward currents that flow through Aleutian passes typically flow down the western side of the pass, whereas northward flow occurs on the eastern side (Stabeno et al., 2005). Because the dominant current along the south side of the Aleutian chain is to the west and the dominant current along the north side is to the east, larval retention zones could exist near passes (Stockhausen and Hermann, 2007). Genetic studies of Pacific ocean perch in other areas have indicated that stock structure on a small scale (70–400 km) may occur and could be the result of limited dispersal of early life stages (Seeb and Gunderson, 1988; Withler et al., 2001; Palof et al., 2011). The possibility for high productivity and larval retention around Aleutian passes, combined with the potential natural barriers to migration of Pacific ocean perch along the archipelago (e.g., predominant currents as well as deeper passes in the western Aleutian Islands), could further explain our results that indicate increases in presence and abundance near Aleutian passes.

The structural heterogeneity created in trawlable habitats by the presence of sponges, corals, and bryozoans presumably provides refugia from predation and shelter from currents for juvenile Pacific ocean perch (Stoner, 1982; Ryer, 1988; Ryer et al., 2004) and recently has been shown to provide nursery habitat for redfish larvae (*Sebastes* spp.) around sea pens (Baillon

et al., 2013). Juvenile Pacific ocean perch have been observed in close association with sponges and corals on the bottom (Carlson and Straty, 1981; Rooper et al., 2007) and appear to favor more spatially heterogeneous habitats (Du Preez and Tunnicliffe, 2011). Adult Pacific ocean perch are known to form schools on or near the seafloor (Krieger, 1993; Brodeur, 2001; Hanselman et al., 2012) where we typically collect them over areas of softer seafloor substrata, such as sand or gravel, during our surveys. Adults have been observed in association with sea whip forests (Brodeur, 2001), although they appear, on the basis of our model results, to be less benthically oriented than juveniles. The apparent affiliation of Pacific ocean perch with biogenic structures over trawlable habitats in the Aleutian Islands could potentially modify their distribution and abundance patterns on a local scale within the context of the broadly acting biological and oceanographic processes that determine larger scale patterns.

All our models retained biogenic structures with morphological features capable of increasing structural heterogeneity in the otherwise low-relief, trawlable habitats, but none retained the Sp predictor, the presence–absence factor compositely representing all sponges. Most of the sponges and corals retained in our models are erect forms (e.g., V and F sponges and primnoid corals), but even the nonerect forms (e.g., G and Gp sponges) are known to be epizoic on larger, erect sponge forms (Stone et al., 2011). In previous studies that showed associations of *Sebastes* species (Heifetz, 2002; Krieger and Wing, 2002; Du Preez and Tunnicliffe, 2011) and Pacific ocean perch (Rooper and Boldt, 2005; Rooper et al., 2007) with sponges and corals, the epibenthic invertebrates were considered composite categories. The results of our study refine our understanding of the relationship between Pacific ocean perch distribution and abundance and the structural heterogeneity provided by biogenic structures from these larger composite groupings. Our results indicate that habitat heterogeneity, and vertical relief in particular, can affect Pacific ocean perch distribution and abundance.

Although studies have indicated that the presence of structure-forming epibenthic invertebrates can lead to enhanced abundance and biodiversity of associated animals (e.g., Du Preez and Tunnicliffe, 2011; Beazley et al., 2013; Knudby et al., 2013), Tissot et al. (2006) concluded that associations of fishes with sponges and corals do not necessarily imply functional relationships between these groups of organisms. The co-occurrences between Pacific ocean perch and biogenic structures that we modeled in the Aleutian Islands may derive from facultative relationships (e.g., structural refugia and prey availability) or could simply result from a convergence of conditions that favor the presence of both the fish and epibenthic invertebrates. The underlying mechanisms leading to the patterns observed in our study are an important area for future study.

Generalized additive models relate response variables to dependent model variables through additive and unrestrictive smooth functions, making them well suited for modeling typical interactions of species with environment (Hastie and Tibshirani, 1986; Maravelias, 2001; Guisan et al., 2002). The GAMs also provide a data-defined assessment of the shape of the response of a species to independent variables (Maravelias and Papaconstantinou, 2003). The anticipated nonlinear relationships of Pacific ocean perch distribution and abundance with their environment made GAMs well suited to provide a tool that was more informative than traditional regression techniques.

One drawback to the use of GAMs is that they can over-fit the data, resulting in unrealistic models with limited predictive power (Kim and Gu, 2004; Wood, 2006). To minimize the risk of over-fitting, we constrained the df available to smoothed continuous predictor variables in the model and successfully validated our GAM predictions of juvenile and adult presence with a data set external to the modeling effort (i.e., the data from the 2012 Aleutian Islands trawl survey). We conclude that the GAMs parameterized in this study were fairly accurate predictors of juvenile occurrence but were better at predicting adult occurrence. Furthermore, our validation results indicate that these models were robust predictors of the distribution and abundance of Pacific ocean perch juveniles and adults in the Aleutian Islands in subsequent years.

Our approach of modeling presence and absence and conditional abundance independently is a technique intended to cope with zero-inflated and over-dispersed data and that is common to abundance surveys (McCullagh and Nelder, 1989; Barry and Welsh, 2002). Processes that influence distribution and those that affect abundance do not have to be the same. By modeling the 2 response variables independently, we were able to determine that the models for Pacific ocean perch distribution and conditional abundance shared more in common than not. For example, the best-fitting models for both life stages across both model classes all share the D,T and Long. terms in common, but for the presence–absence GAMs adults and juveniles also share the Sl and V_T terms. By comparison, there is no overlap in the suite of biogenic structures retained in the juvenile presence–absence and conditional abundance GAMs, a result that may indicate that the local conditions leading to enhanced probability of encountering juvenile Pacific ocean perch in our trawl tows are not the same as those leading to increased abundance when this species is present.

There is ample evidence that rockfishes occur commonly in areas that are untrawlable with our present net (Carlson and Haight, 1976; Zimmermann, 2003; Rooper et al., 2007; Rooper et al., 2011). Underwater camera and submersible observations indicate that some untrawlable areas are havens for biogenic structures and fishes (Rooper et al., 2007; Stone et al., 2011). In some instances, catch rates for Pacific ocean perch varied with tidal velocity (i.e., juvenile and adult occurrence). Changing catch rates could result from tidal current regimes that affect distribution and abundance

of Pacific ocean perch directly (e.g., currents that exceed swimming speeds) or indirectly by impacting biogenic structures that would otherwise provide refugia from currents (e.g., physical removal of structures in high current areas or their morphological adaptation to differing local current or sedimentation regimes). We hope to use in situ observation of current speeds and fish behavior (e.g., optical sampling) over trawlable and untrawlable bottom in the future, along with direct measurements of water velocity into the net mouth, to try and elucidate some of the potential mechanisms of this phenomenon and to improve the predictive power of these models.

We were not able to account for all of the variables that may influence the distribution and abundance of Pacific ocean perch in the Aleutian Islands. Among these variables were the availability of prey and the substrate type at each bottom trawl survey station. Both of these factors are known to influence the distribution and abundance of rockfishes (Carlson and Straty, 1981; Pearcy et al, 1989; Matthews, 1990; Love et al., 1991; Stein et al., 1992; Krieger and Ito, 1999; Yoklavich et al., 2000; Boldt and Rooper, 2009). Pacific ocean perch feed primarily on copepods and euphasiids both as juveniles and adults (Carlson and Haight, 1976; Brodeur, 1983; Boldt and Rooper 2009), and the success of these predator–prey interactions is concentration dependent and partly mediated by the availability of light that enables a fish to locate its prey. Water column light (irradiance) profiles vary widely across the Aleutian Islands (senior author, unpubl. data). Fish species are known to change their behavior in response to changing ambient light levels (e.g., Ryer and Olla, 1999; Kotwicki et al., 2009). The amount and spectral range of the available light in the water column may be another important component of EFH for fish with visually mediated behaviors (Sathyendranath and Platt, 1990). Incorporating irradiance and spectral quality of light as habitat parameters in future models will provide new insights into delineating fish habitats.

Effective management of fish populations and fishing activities requires better knowledge of the functional relationships between fish species and their habitats. In the case of Pacific ocean perch, we have concluded from this study that the species occurs predictably within certain depth ranges, in certain areas, and that they can be associated with erect forms of sponges and corals. In the Aleutian Islands, fishing activities can affect benthic habitats by causing damage and mortality to sponges and corals. A number of studies have shown that recovery times for sponges and corals damaged by bottom trawling or natural phenomena could be on the order of decades to centuries (Freese et al., 1999; Andrews et al., 2002; Rooper et al., 2011). Diagnosing the relationships between commercially important fish species and biogenic structures vulnerable to damage from human activity will be useful for management decisions to balance habitat protection and commercial fishing opportunities.

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Literature cited

Andrews, A. H., E. E. Cordes, M. M. Mahoney, K. Munk, K. H. Coale, G. M. Cailliet, and J. Heifetz.
2002. Age, growth and radiometric age validation of a deep-sea, habitat-forming, gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska. Hydrobiologia 471:101–110.

Baillon, S., J. Hamel, V. Wareham, and A. Mercier.
2012. Deep cold-water corals as nurseries for fish larvae. Front. Ecol. Environ. 10:351–356.

Barry, S. C., and A. H. Welsh.
2002. Generalized additive modelling and zero inflated count data. Ecol. Model. 157:179–188.

Barthel, D.
1997. Fish eggs and pentacrinoids in Weddell Sea hexactinellids: further examples for the structuring role of sponges in Antarctic benthic ecosystems. Polar Biol. 17(1):91–94.

Beazley, L. I., E. L. Kenchington, F. J. Murillo, and M. del Mar Sacau.
2013. Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic. ICES J. Mar. Sci. 70:1471–1490.

Bell, J. J., and D. K. A. Barnes.
2000. The influences of bathymetry and flow regime upon the morphology of sublittoral sponge communities. J. Mar. Biol. Assoc. U.K. 80:707–718.
2001. Sponge morphological diversity: a qualitative predictor of species diversity? Aquat. Conserv.: Mar. Freshw. Ecosyst. 11:109–121.

Boldt, J. L., and C. N. Rooper.
2009. Abundance, condition, and diet of juvenile Pacific ocean perch (*Sebastes alutus*) in the Aleutian Islands. Fish. Bull. 107:278–285.

Boury-Esnault, N., and K. Rützler (eds.).
1997. Thesaurus of sponge morphology. Smithson. Contrib. Zool. 596, 59 p. Smithsonian Inst. Press, Washington, D.C.

Brodeur, R. D.
1983. Food habits, dietary overlap and gastric evacuation rates of rockfishes (genus *Sebastes*). M. S. thesis, 96 p. Oregon State Univ., Corvalis, OR. [Available at website.]
2001. Habitat-specific distribution of Pacific ocean perch (*Sebastes alutus*) in Pribilof Canyon, Bering Sea. Cont. Shelf Res. 21:207–224.

Carlson, H. R., and R. E. Haight.
1976. Juvenile life of Pacific ocean perch (*Sebastes alutus*) in coastal fjords of southeastern Alaska: their environment, growth, food habits, and schooling behavior. Trans. Am. Fish. Soc. 105:191–201.

Carlson, H. R., and R. R. Straty.
1981. Habitat and nursery grounds of Pacific rockfish, *Sebastes* spp., in rocky coastal areas of southeastern Alaska. Mar. Fish. Rev. 43(7):13–19.

Chikuni, S.
1975. Biological study on the population of the Pacific ocean perch in the North Pacific. Bull. Far Seas Fish. Res. Lab. 12:1–119.

Cochran, W. G.
1977. Sampling techniques, 3rd ed., 428 p. John Wiley & Sons, Inc., New York.

Coker, D. J., S. K. Wilson, and M. S. Pratchett.
2014. Importance of live coral habitat for reef fishes. Rev. Fish Biol. Fish. 24:89–126.

Coyle, K. O.
2005. Zooplankton distribution, abundance and biomass relative to water masses in eastern and central Aleutian Island passes. Fish. Oceanogr. 14(suppl. 1):77–92.

Dayton, P. K., G. A. Robilliard, R. T. Paine, and L. B. Dayton.
1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol. Monogr. 44:105–128.

Du Preez, C., and V. Tunnicliffe.
2011. Shortspine thornyhead and rockfish (Scorpaenidae) distribution in response to substratum, biogenic structures and trawling. Mar. Ecol. Prog. Ser. 425:217–231.

Egbert, G. D., A. F. Bennett, and M. G. G. Foreman.
1994. TOPEX/POSEIDON tides estimated using a global inverse model. J. Geophys. Res. 99:24821–24852.

Egbert, G. D., and S. Y. Erofeeva.
2002. Efficient inverse modeling of barotropic ocean tides. J. Atmos. Ocean. Technol. 19:183–204.

Engel, J., and R. Kvitek.
1998. Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. Conserv. Biol. 12:1204–1214.

Freese, J. L.
2001. Trawl-induced damage to sponges observed from a research submersible. Mar. Fish. Rev. 63(3):7–13.

Freese, L., P. J. Auster, J. Heifetz, and B. L. Wing.
1999. Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. Mar. Ecol. Prog. Ser. 182:119–126.

Freese, J. L., and B. L. Wing.
2003. Juvenile red rockfish, *Sebastes* sp., associations with sponges in the Gulf of Alaska. Mar. Fish. Rev. 65(3):38–42.

Greene, G. H., V. M. O'Connell, and C. K. Brylinsky.
2011. Tectonic and glacial related seafloor geomorphology as possible demersal shelf rockfish habitat surrogates—Examples along the Alaskan convergent transform plate boundary. Cont. Shelf Res. 31:S39–S53.

Guisan, A., T. C. Edwards, Jr., and T. Hastie.
2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model. 157:89–100.

Hanselman, D. H., P. D. Spencer, D. R. McKelvey, and M. H. Martin.
2012. Application of an acoustics-trawl survey design to improve estimates of rockfish biomass. Fish. Bull. 110:379–396.

Hastie, T., and R. Tibshirani.
1986. Generalized additive models. Stat. Sci. 1:297–318.

Heifetz, J.
2002. Coral in Alaska: distribution, abundance, and species associations. Hydrobiologia 471:19–28.

Heifetz, J., B. L. Wing, R. P. Stone, P. W. Malecha, and D. L. Courtney.
2005. Corals of the Aleutian Islands. Fish. Oceanogr. 14(suppl. 1):131–138.

Hourigan, T. F.
2009. Managing fishery impacts on deep-water coral ecosystems of the USA: emerging best practices. Mar. Ecol. Prog. Ser. 397:333–340.

Kim, Y.-J., and C. Gu.
2004. Smoothing spline Gaussian regression: more scalable computation via efficient approximation. J. R. Stat. Soc., Ser. B: Stat. Method. 66:337–356.

Knudby, A., E. Kenchington, and F. J. Murillo.
2013. Modeling the distribution of *Geodia* sponges and sponge grounds in the Northwest Atlantic. PLoS ONE 8(12):e82306.

Kotwicki, S., A. DeRobertis, P. von Szalay, and R. Towler.
2009. The effect of light intensity on the availability of walleye pollock (*Theragra chalcogramma*) to bottom trawl and acoustic surveys. Can. J. Fish. Aquat. Sci. 66:983–994.

Krebs, C. J.
1989. Ecological methodology, 2nd ed., 654 p. Harper & Row, Publs., Inc., New York.

Krieger, K. J.
1993. Distribution and abundance of rockfish determined from a submersible and by bottom trawling. Fish. Bull. 91:87–96.

Krieger, K. J., and D. H. Ito.
1999. Distribution and abundance of shortraker rockfish, *Sebastes borealis*, and rougheye rockfish, *S. aleutianus*, determined from a manned submersible. Fish. Bull. 97:264–272.

Krieger, K. J., and B. L. Wing.
2002. Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. Hydrobiologia 471:83–90.

Ladd, C., G. L. Hunt Jr., C. W. Mordy, S. A. Salo, and P. J. Stabeno.
2005. Marine environment of the eastern and central Aleutian Islands. Fish. Oceanogr. 14(suppl. 1):22–38.

Laidig, T. E., D. L. Watters, and M. M. Yoklavich.
2009. Demersal fish and habitat associations from visual surveys on the central California shelf. Estuar. Coast. Shelf Sci. 83:629–637.

Landis, J. R., and G. G. Koch.
1977. The measurement of observer agreement for categorical data. Biometrics 33:159–174. [Available at website.]

Logerwell, E. A., K. Aydin, S. Barbeaux, E. Brown, M. E. Conners, S. Lowe, J. W. Orr, I. Ortiz, R. Reuter, and P. Spencer.
2005. Geographic patterns in the demersal ichthyofauna of the Aleutian Islands. Fish. Oceanogr. 14(suppl. 1):93–112.

Love, M. S., M. H. Carr, and L. Haldorson.
1991. The ecology of substrate-associated juveniles of the genus *Sebastes*. Environ. Biol. Fish. 30:225–243.

Love, M. S., M. Yoklavich, and L. Thorsteinson.
2002. The rockfishes of the northeast Pacific, 414 p. Univ. California Press, Berkeley, CA.

Malecha, P. W., R. P. Stone, and J. Heifetz.
2005. Living substrate in Alaska: Distribution, abundance, and species associations. Am. Fish. Soc. Symp. 41:289–299.

Manel, S., H. Ceri Williams, and S. J. Ormerod.
2001. Evaluating presence–absence models in ecology: the need to account for prevalence. J. Appl. Ecol. 38:921–931.

Maravelias, C. D.
2001. Habitat associations of Atlantic herring in the Shetland area: influence of spatial scale and geographic segmentation. Fish. Oceanogr. 10:259–267.

Maravelias, C., and C. Papaconstantinou.
2003. Size-related habitat use, aggregation patterns and abundance of anglerfish (*Lophius budegassa*) in the Mediterranean Sea determined by generalized additive modelling. J. Mar. Biol. Assoc. U.K. 83:1171–1178.

Marliave, J., and W. Challenger.
2009. Monitoring and evaluating rockfish conservation areas in British Columbia. Can. J. Fish. Aquat. Sci. 66:995–1006.

Matthews, K. R.
1990. A comparative study of habitat use by young-of-the-year, subadult, and adult rockfishes on four habitat types in central Puget Sound. Fish. Bull. 88:223–239.

McCullagh, P., and J. A. Nelder.
1989. Generalized linear models, 2nd ed, 532 p. Chapman and Hall, London.

O'Brien, L., and P. Rago.
1996. An application of the generalized additive model to groundfish survey data with Atlantic cod off the northeast coast of the United States as an example. NAFO Sci. Counc. Stud. 28:79–95. [Available at website.]

Palof, K. J., J. Heifetz, and A. J. Gharrett.
2011. Geographic structure in Alaskan Pacific ocean perch (*Sebastes alutus*) indicates limited lifetime dispersal. Mar. Biol. 158:779–792.

Palumbi, S. R.
1984. Tactics of acclimation: morphological changes of sponges in an unpredictable environment. Science 225:1478–1480.

Paraketsov, I. A.
1963. On the biology of *Sebastodes alutus* of the Bering Sea. *In* Soviet fisheries investigations in the northeastern Pacific, part I (P. A. Moiseev, ed.), p. 319–327. [Available from U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA, as TT67-51203.]

Pearcy, W. G., D. L. Stein, M. A. Hixon, E. K. Pikitch, W. H. Barss, and R. M. Starr.
1989. Submersible observations of deep-reef fishes of Heceta Bank, Oregon. Fish. Bull. 87:955–965.

R Development Core Team.
2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from http://www.r-project. org, accessed August, 2011.]

Rand, K. M., and S. A. Lowe.
2011. Defining essential fish habitat for Atka mackerel with respect to feeding within and adjacent to Aleutian Islands trawl exclusion zones. Mar. Coast. Fish. 3:21–31.

Rooper, C. N.
2008. An ecological analysis of rockfish (*Sebastes* spp.) assemblages in the North Pacific Ocean along broad-scale environmental gradients. Fish. Bull. 106:1–11.

Rooper, C. N., and J. L. Boldt.
2005. Distribution of juvenile Pacific ocean perch *Sebastes alutus* in the Aleutian Islands in relation to benthic habitat. Alaska Fish. Res. Bull. 11:102–112.

Rooper, C. N., J. L. Boldt, and M. Zimmermann.
2007. An assessment of juvenile Pacific ocean perch (*Sebastes alutus*) habitat use in a deepwater nursery. Estuar. Coast. Shelf Sci. 75:371–380.

Rooper, C. N., G. R. Hoff, and A. De Robertis.
2010. Assessing habitat utilization and rockfish (*Sebastes* spp.) biomass on an isolated rocky ridge using acoustics and stereo image analysis. Can. J. Fish. Aquat. Sci. 67:1658–1670.

Rooper, C. N., and M. H. Martin.
2009. Predicting presence and abundance of demersal fishes: a model application to shortspine thornyhead *Sebastolobus alascanus*. Mar. Ecol. Prog. Ser. 379:253–266.
2012. Comparison of habitat-based indices of abundance with fishery-independent biomass estimates from bottom trawl surveys. Fish. Bull. 110:21–35.

Rooper, C. N., and M. E. Wilkins.
2008. Data report: 2004 Aleutian Islands bottom trawl survey. NOAA Tech. Memo. NMFS-AFSC-185, 207 p. [Available at website]

Rooper, C. N., M. E. Wilkins, C. S. Rose, and C. Coon.
2011. Modeling the impacts of bottom trawling and the subsequent recovery rates of sponges and corals in the Aleutian Islands, Alaska. Cont. Shelf Res. 31:1827–1834.

Ryer, C. H.
1988. Pipefish foraging: effects of fish size, prey size and altered habitat complexity. Mar. Ecol. Prog. Ser. 48:37–45.

Ryer, C. H., and B. L. Olla.
1999. Light-induced changes in prey consumption and behavior of two juvenile planktivorous fish. Mar. Ecol. Prog. Ser. 181:41–51.

Ryer, C. H., A. W. Stoner, and R. H. Titgen.
2004. Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. Mar. Ecol. Prog. Ser. 268:231–243.

Sathyendranath, S., and T. Platt.
1990. The light field in the ocean: its modification and exploitation by the pelagic biota. Light and life in the sea (P. J. Herring, A. K. Campbell, M. Whitfield, and L. Maddox, eds.) p. 3–18. Cambridge Univ. Press, Cambridge, UK.

Seeb, L. W., and D. R. Gunderson.
1988. Genetic variation and population structure of Pacific ocean perch (*Sebastes alutus*). Can. J. Fish. Aquat. Sci. 45:78–88.

Stabeno, P. J., D. G. Kachel, N. B. Kachel, and M. E. Sullivan.
2005. Observations from moorings in the Aleutian Passes: temperature, salinity and transport. Fish. Oceanogr. 14(suppl. 1):39–54.

Stabeno, P. J., J. D. Schumacher, and K. Ohtani.
1999. The physical oceanography of the Bering Sea. *In* Dynamics of the Bering Sea: a summary of physical, chemical, and biological characteristics, and a synopsis of research on the Bering Sea (T. R. Loughlin and K. Ohtani, eds.), p. 1–28. Alaska Sea Grant College Program Rep. AK-SG-99-03. Univ. Alaska, Fairbanks, AK.

Stauffer, G.
2004. NOAA protocols for groundfish bottom trawl surveys of the nation's fishery resources. NOAA Tech. Memo. NMFS-F/SPO-65, 205 p. [Available at website.]
Stein, D. L., B. N. Tissot, M. A. Hixon, and W. Barss.
1992. Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. Fish. Bull. 90:540–551.
Stockhausen, W. T., and A. J. Hermann.
2007. Modeling larval dispersion of rockfish: a tool for marine reserve design? *In* Biology, assessment, and management of North Pacific rockfishes (J. Heifetz, J. DiCosimo, A. J. Gharrett, M. S. Love, V. M. O'Connell, and R. D. Stanley, eds.), Alaska Sea Grant College Program Rep. AK-SG-07-01. Univ. Alaska, Fairbanks, AK.
Stone, R., H. Lehnert, and H. Reiswig.
2011. A guide to the deep-water sponges of the Aleutian Island Archipelago. NOAA Professional Paper NMFS 12, 187 p.
Stoner, A. W.
1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linnaeus). J. Exp. Mar. Biol. Ecol. 58:271–284.
Swift, J., and K. Aagaard.
1976. Upwelling near Samalga Pass. Limnol. Oceanogr. 21:399–408.
Tissot, B. N., M. M. Yoklavich, M. S. Love, K. York, and M. Amend.
2006. Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral. Fish. Bull. 104:167–181.
von Szalay, P. G., C. N. Rooper, N. W. Raring, and M. H. Martin.
2011. Data report: 2010 Aleutian Islands bottom trawl survey. NOAA Tech. Memo. NMFS-AFSC-215, 153 p. [Available at website.]
Wakabayashi, K., R. G. Bakkala, and M. S. Alton.
1985. Methods of the U.S.–Japan demersal trawl surveys. *In* Results of cooperative U.S.–Japan groundfish investigations in the Bering Sea during May–August 1979 (R. G. Bakkala and K. Wakabayashi eds.), p. 7–29. INPFC Bull. 44. [Available at website.]
Wassenberg, T. J., G. Dews, and S. D. Cook.
2002. The impact of fish trawls on megabenthos (sponges) on the north-west shelf of Australia. Fish. Res. 58: 141–151.
Weinberg, K. L., and S. Kotwicki.
2008. Factors influencing net width and sea floor contact of a survey bottom trawl. Fish. Res. 93:265–279.
Wing, B. L., and D. R. Barnard.
2004. A field guide to Alaskan corals. NOAA Tech. Memo. NMFS-AFSC 146, 67 p. [Available at website.]
Withler, R. E., T. D. Beacham, A. D. Schulze, L. J. Richards, and K. M. Miller.
2001. Co-existing populations of Pacific ocean perch, *Sebastes alutus*, in Queen Charlotte Sound, British Columbia. Mar. Biol. 139:1–12.
Wood, S. N.
2006. Generalized additive models: an introduction with R, 392 p. Chapman and Hall/CRC, Boca Raton, FL.
Yoklavich, M. M., H. G. Greene, G. M. Cailliet, D. E. Sullivan, R. N. Lea, and M. S. Love.
2000. Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. Fish. Bull. 98:625–641.
Zar, J. H.
1984. Biostatistical analysis, 2nd ed., 718 p. Prentice-Hall, Inc., Englewood, NJ.
Zenger, H. H., Jr.
2004. Data report: 2002 Aleutian Islands bottom trawl survey. NOAA Tech. Memo. NMFS-AFSC-143, 247 p. [Available at Website.]
Zimmermann, M.
2003. Calculation of untrawlable areas within boundaries of a bottom trawl survey. Can. J. Fish. Aquat. Sci. 60:657–669.
Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith.
2009. Mixed effects models and extensions in ecology with R, 596 p. Springer, New York.

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Diet composition, feeding strategy, and diet overlap of 3 sciaenids along the southeastern United States

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Abstract—From 2008 through 2010, the diets of 3 sciaenid species, the weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*), were examined. Stomach contents were identified, enumerated, and weighed to determine the diet composition and feeding strategy of each species and diet overlap among species. Bony fishes were the most frequently consumed prey of weakfish. Decapods, nondecapod crustaceans, and polychaetes were the most commonly consumed prey of southern kingfish and Atlantic croaker. Some individuals of all species consumed specific prey types and others consumed varying prey types; however, specialization was a more common trait for weakfish than for the other 2 species. Weakfish diets had minimal overlap with diets of the other 2 species; however, the Morisita-Horn index indicated considerable overlap between southern kingfish and Atlantic croaker. Potential for competition could occur between these 2 species, but, because both are often opportunistic feeders, it is unlikely that competition would occur unless shared resources become scarce. Descriptions of feeding strategies, prey resources, and the potential for competition among co-occurring species can provide a framework for management of these species, particularly for ecosystem-based management.

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Ecosystem-based fisheries management is dependent on defining not only target species but the species and habitats with which they interact. Ecosystem-based management models ideally would account for the complexities of ecosystems, allowing managers to incorporate ecosystem relationships in management strategies and decisions (Brodziak and Link, 2002). The Magnuson-Stevens Fishery and Conservation Reauthorization Act of 2006 (Magnuson-Stevens...Act, 2007) highlighted the need for research detailing interdependence among fisheries; trophic relationships can play a key role in understanding ecosystem composition, status, and energy linkages within the system (Link, 2002; Magnuson-Stevens...Act, 2007; Ainsworth et al., 2008). As a result, the South Atlantic Fishery Management Council (SAFMC) has prioritized efforts to characterize fish diets, define relationships between predator and prey, and to better understand how these relationships affect economically important species (SAFMC[1]). Therefore, the South Atlantic component of the Southeast Area Monitoring and Assessment Program (SEAMAP-SA), as part of its Coastal Survey (a long-term, fishery-independent, shallow-water trawl survey from Cape Canaveral, Florida, to Cape Hatteras, North Carolina), began collecting stomachs from 3 common species of Sciaenidae: weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*).

Weakfish, southern kingfish, and Atlantic croaker commonly occur along the eastern coast of the United States, residing in shallow waters over bottoms of sand or sandy mud. Distributions of these species greatly overlap, sharing a geographic range from Cape Cod, Massachusetts, to Florida and into the Gulf of Mexico (only occasionally in the Gulf of Mexico in the case of weakfish) (Goode,

[1] SAFMC (South Atlantic Fishery Management Council). 2009. Fishery Ecosystem Plan of the South Atlantic Region. Volume V: South Atlantic research programs and data needs, 177 p. South Atlantic Fishery Management Council, North Charleston, SC. [Available at website.]

1884; Chao, 2002). In the southeastern United States, these species have a similar life history; they grow rapidly and are capable of spawning as early as 1 year of age (Walton, 1996).

Weakfish generally spawn from March through July in estuarine and nearshore waters, and juveniles use the estuary as nursery grounds. From 2008 through 2010, weakfish with an average age <1 year old and a mean of 21 cm in total length (TL) were captured in SEAMAP-SA trawl surveys, but this species reportedly lives to 8 years and can reach a length of 90 cm TL (Shepherd and Grimes, 1983; Chao, 2002). Adult weakfish migrate seasonally between nearshore and offshore waters, and forage throughout the water column.

Southern kingfish are bottom foragers that spawn on the continental shelf from April through August, live up to 6 years, and can grow to lengths of 60 cm TL (Bearden, 1963; Smith and Wenner, 1985; Chao, 2002). For southern kingfish captured by SEAMAP-SA from 2008 to 2010, the average age was 1 year and the average size was 18 cm TL. Atlantic croaker are shelf-spawners during October–January and can reach an age of 15 years and length of 46 cm TL (Hales and Reitz, 1992; Barbieri et al., 1994; Richardson and Boylan[2]). From 2008 to 2010, the mean age and length for specimens of Atlantic croaker collected by SEAMAP-SA were 1 year and 22 cm TL, respectively. Atlantic croaker are demersal and use their inferior-located mouth to suck prey from the substrate (Overstreet and Heard, 1978). Juveniles of both southern kingfish and Atlantic croaker use estuaries as nurseries, a characteristic similar to weakfish (Musick and Wiley, 1972; Harding and Chittenden, 1987).

Although the life history of these 3 species has been studied extensively, quantitative diet information from the southeastern United States is either lacking or was collected 2 or more decades ago. The potential for diet overlap among sciaenids with similar feeding strategies has not been addressed in this region to date. Merriner (1975) examined the diet of weakfish captured in North Carolina waters and found that penaeid and mysid shrimps, anchovies, and clupeid fishes were the most common food items. He noted a gradual ontogenetic shift from shrimp to clupeids, specifically the Atlantic thread herring (*Opisthonema oglinum*), beginning when weakfish were about 19 cm standard length (SL) and 1 year of age. McMichael and Ross (1987) analyzed the diets of southern kingfish, northern kingfish (*Menticirrhus saxatilis*), and gulf kingfish (*M. littoralis*) in the Gulf of Mexico and found that southern kingfish most frequently consume bivalve siphons and cumaceans, followed by mysids, polychaetes, brachyurans, and gammarid amphipods. Although frequency of prey items seemed to be dependent on season, prey item composition was not found to be significantly different among species within a season in that study. A diet study of species of *Menticirrhus*, conducted near the Patos Lagoon in Brazil, has shown both low species diversity and seasonal differences in prey consumption, with polychaetes, amphipods, and various crustaceans being consumed most frequently (Rodrigues and Vieira, 2010). Overstreet and Heard (1978) studied Atlantic croaker diets in the Gulf of Mexico and found a high diversity of prey items, including polychaetes, mysids, blue crabs, amphipods, and penaeids, among other prey items.

Each of these fish species is important both commercially and recreationally, and each commonly occurs as bycatch in the shrimp trawl fishery (Smith and Wenner, 1985; Murray et al., 1992; Diamond et al., 2000). In addition, Atlantic croaker is harvested for use in the bait industry (Ross, 1988). Management of these species has become necessary as these industries evolve and catch levels increase.

We investigated the diets of weakfish, southern kingfish, and Atlantic croaker off the southeastern United States to provide current regional information on their diets. We also assessed the overlap in prey among the 3 species and examined several factors that may influence this assessment, including spatial and temporal variation in sampling.

Materials and methods

Field sampling

Fishes were collected from 2008 to 2010 during shallow-water trawl hauls conducted as part of the SEAMAP-SA Coastal Survey by staff of the South Carolina Department of Natural Resources. Paired 22.9-m mongoose-type Falcon[3] trawl nets (Beaufort Marine Supply, Beaufort, SC), which had a net body of no. 15 twine with 4.8-cm stretch mesh and a cod end of no. 30 twine with 4.1-cm stretch mesh, were deployed from the RV *Lady Lisa*, a 23-m wooden-hulled, double-rigged St. Augustine Trawlers (St. Augustine Trawlers Inc., St. Augustine, FL) shrimp trawler. Trawl hauls were conducted during daylight hours at target speeds of 1.3 m/s (2.5 kn) for 20 min and at depths between 4 and 10 m (Hendrix and Boylan[4]). For the Coastal Survey, trawl hauls are conducted at randomly selected locations within 6 regions from Cape Canaveral, Florida, to Cape Hatteras, North Carolina (Fig. 1). Regions are

[2] Richardson, J., and J. Boylan. 2013. Results of trawling efforts in the coastal habitat of the South Atlantic Bight, 2012. Report SEAMAP-SA-CS-2012-004, 101 p. [Available from Mar. Resour. Res. Inst., Mar. Resour. Div., South Carolina Dep. Natl. Resour. 217 Fort Johnson Rd., Charleston, SC 29422.]

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4] Hendrix, C., and J. Boylan. 2011. Results of trawling efforts in the coastal habitat of the South Atlantic Bight, 2010. Report SEAMAP-SA-CS-2010-004, 108 p. [Available from Mar. Resour. Res. Inst., Mar. Resour. Div., South Carolina Dep. Nat. Resour, 217 Fort Johnson Rd., Charleston, SC 29422.]

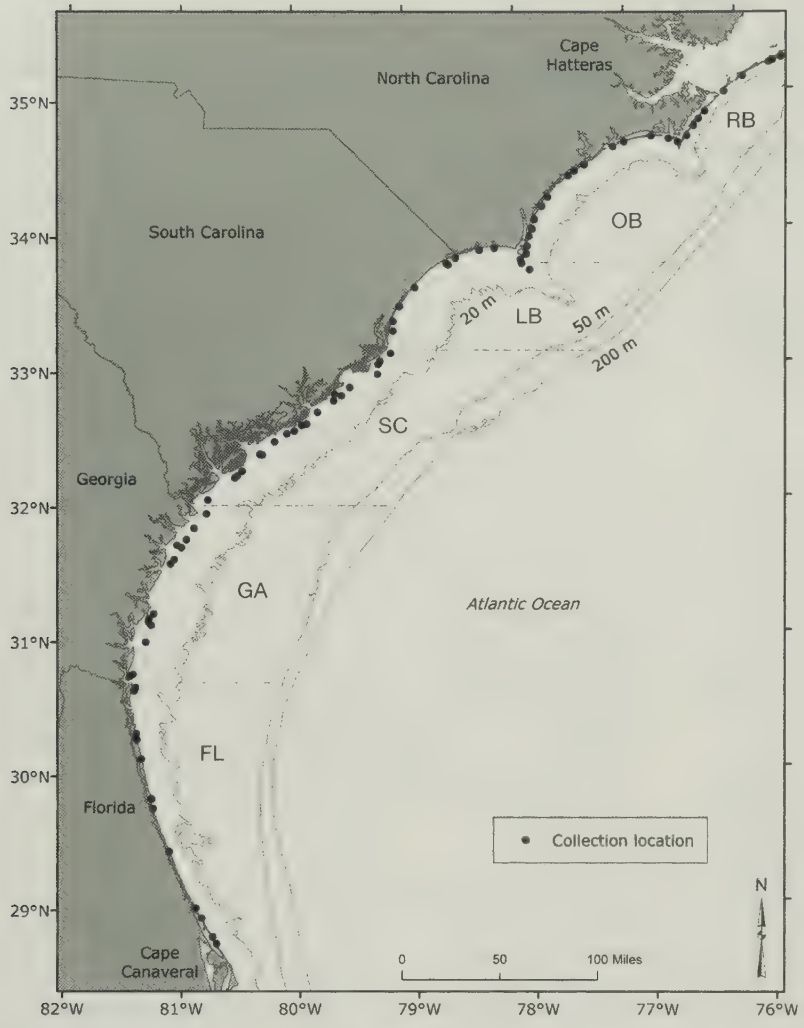

Figure 1

Map of the sampling area of the Coastal Survey of the Southeastern Monitoring and Assessment Program—South Atlantic off the southeastern coastline of the United States, extending from Cape Canaveral, Florida, to Cape Hatteras, North Carolina. The sampling area is divided into 6 regions: Florida (FL), Georgia (GA), South Carolina (SC), Long Bay (LB), Onslow Bay (OB), and Raleigh Bay (RB). Black circles indicate locations where 3 sciaenid fishes— weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*)—were collected from 2008 through 2010 for analysis of their stomach contents.

divided further into strata based on latitude (~0.28° latitude; 2–5 strata per region). The Coastal Survey includes 3 cruises conducted each year during 3 seasons: spring (April–May), summer (July–August), and fall (September–November). Specimens retained for life history research (including diet analysis) were selected from the total catches at a rate of 2 representatives per size class (based on TL in centimeters) per stratum per season. Fish were kept on ice on deck until sample processing began. Total length (in millimeters), SL (in millimeters) and total body weight (in grams) were measured, and otoliths and gonads were extracted. Stomachs, excluding the intestinal tract, were removed from selected specimens, wrapped in cheesecloth and labeled. Stomachs were stored in 10% neutral buffered formalin for a minimum of 14 days, after which they were rinsed with room temperature tap water several times and stored in 70% ethanol.

Laboratory processing

Extraneous tissue was removed from the stomach, the stomach was blotted to remove excess liquid and emptied, and a wet weight of the contents was recorded to the nearest 0.001 g. Each prey item was identified to the lowest possible taxon that could be collapsed into 7 course prey categories: bony fishes, decapod crustaceans, echinoderms, mollusks, nondecapod crustaceans, polychaetes, and other (composed of unidentified animal tissue and rarely seen miscellaneous taxa). Identifications were made from voucher specimens, with staff assistance from the Southeastern Regional Taxonomic Center, and according to various references (e.g., Baremore and Bethea[5]). Small parts were sorted and counted to estimate numbers of individuals whenever possible. When prey were highly digested, key body parts, such as eyes, telsons, or otoliths, were used to make counts. When the number of individuals could not be determined (e.g., from unidentified animal tissue), a conservative count of one individual was assigned. Prey were collectively weighed by taxon to the nearest 0.001 g.

Data analysis

before any analyses, prey items that could not be identified and stomach contents that were incidentally ingested (e.g., sand and gravel) were removed from the data set. To provide the most conservative estimate of overlap in diet, only stomachs from fish collected in trawl hauls that captured all 3 species were included in analyses. Co-occurrence provides the most likely possibility that shared resources were available to each species, regardless of whether they used them. Diet contents were grouped into the 7 prey categories, initially to reduce the number of zero observations in the data set. Data

[5] Baremore, I. E., and D. M. Bethea. 2011. A guide to otoliths from fishes of the Gulf of Mexico. Panama City Laboratory, NOAA Southeast Fisheries Science Center, Panama City, FL. Last modified 29 August 2011. [Available at website.]

were fourth-root transformed, and cluster analysis and nonmetric multidimensional scaling were performed on the resulting Bray-Curtis dissimilarity matrix (McCune and Grace, 2002; Bozzetti and Schulz, 2004) with the packages labdsv and vegan in R software, vers. 2.15.2 (R Core Team, 2012). Predator species, region, year, and season were examined as categorical variables and water depth (in meters), bottom temperature (in degrees Celsius), and salinity were examined as continuous variables by analysis of similarity.

Three metrics of stomach content by prey category were calculated, as percentages, for each predator species, according to Hyslop (1980), where the total sample was defined as all prey within a given prey category: frequency of occurrence, composition by weight, and composition by number. An index of relative importance (IRI) was determined by combining these metrics to eliminate any biases created when each method is analyzed individually (Goldman and Sedberry, 2010; modified from Pinkas et al., 1971):

$$IRI = (N + W) \times F, \quad (1)$$

where F = frequency of occurrence;
N = composition by number; and
W = composition by weight.

IRI has been included only in tabular form as a method of data comparison across diet studies because it is calculated by combining indices that may produce varying results and, therefore, is not necessarily the most robust representation of diet (Cortés, 1997; Hansson, 1998). To provide a more complete picture of prey consumption by each predator, IRI is presented by year.

In additional, mean percent weight and mean percent number were calculated for each predator according to Chipps and Garvey (2007). Prey were analyzed at the lowest possible taxon, and bootstrapping was used to generate bias-corrected 95% confidence intervals for both means with the package boot in R, (vers. 2.15.2). Prey were then grouped into higher prey categories for the purpose of graphical presentation.

Feeding strategy was determined with the method of Amundsen et al. (1996), modified from the method of Costello (1990), where prey-specific abundance (P_i) is plotted against frequency of occurrence. Expressed as a percentage, prey-specific abundance is a given prey taxon's proportion in relation to all prey items observed in only those predator stomachs that contained the given prey taxon:

$$P_i = \left(\frac{\sum S_i}{\sum S_t}\right) \times 100, \quad (2)$$

where S_i = sum of prey i; and
S_t = sum of all prey items found in only those predator stomachs that contained prey I.

Although the summed variable can be composed of the number or the volume or weight of prey items, we used weight and lowest possible prey taxon. The spread and location of points on an Amundsen plot indicate the feeding strategy of the predator population. Data points that cluster near the top of the y-axis indicate specialized feeding by individuals within the population. A cluster close to the origin describes infrequent consumption of a prey type (i.e., prey types that are not an important part of the predator's diet). Data points that are scattered across the graph indicate that a population cannot be characterized as one that employs a single feeding strategy; a population may be specialized sometimes and generalized at other times. Data points clustered in the upper right quadrant of the graph indicate a population with a specialized feeding strategy, where a high percentage of the population consumes one or more specific prey types.

Potential for trophic overlap among each predator pair was tested on mean percent weight and mean percent number with the simplified Morisita-Horn (M-H) index (O):

$$O = (2\sum_i^n P_{ij}P_{ik}) / (\sum_i^n p_{ij}^2 + p_{ik}^2), \quad (3)$$

where n = the total number of prey item groups;
p_{ij} = the proportion of the prey item i used by predator j; and
p_{ik} = the proportion of the prey item i used by predator k (Wolda, 1981; King and Beamish, 2000).

Both mean percent weight and mean percent number were examined to provide the most robust evidence of potential overlap because both variables are biased when viewed independently owing to the broad range of prey sizes (Graham et al., 2007). The M-H index ranges from 0 to 1, with diet overlap increasing as the index approaches 1 (Zaret and Rand, 1971; Labropoulou and Eleftheriou, 1997; King and Beamish, 2000; Graham et al., 2007; Rodrigues and Vieira, 2010).

Results

Analysis of similarity revealed that differences among predator species were significant (goodness of fit: coefficient of determination [r^2]=0.112, P=0.001); however, for a given predator, the differences among years, regions, and seasons were not statistically significant and depth, temperature, and salinity were not correlated with diet composition. Therefore, for the remainder of the analyses, we combined seasons and regions to investigate differences in diet composition among predators and combined years for all analyses except IRI.

Weakfish

For this study, 349 individuals with an average size of 21 cm TL for young-of-the-year fish through adult fish, were examined. Of the 349 stomachs extracted, 276 contained food (79%; Table 1) and prey represented 71 taxa (Table 2).

Table 1

Number of stomachs extracted for this study, according to year, region, and season, from weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*) collected from 2008 through 2010 during nearshore trawl surveys conducted by the Southeastern Monitoring and Assessment Program—South Atlantic.

	2008			2009			2010		
	Weakfish	Southern kingfish	Atlantic croaker	Weakfish	Southern kingfish	Atlantic croaker	Weakfish	Southern kingfish	Atlantic croaker
Spring									
Region									
Florida	5	5	1	4	2	7	7	23	6
Georgia	1	4	1	2	6	6			
South Carolina	1	8	3						
Long Bay				11	14	7	1	6	4
Onslow Bay				9	15	8	15	20	9
Raleigh Bay				8	9	8	16	25	4
All areas	7	17	5	34	46	36	39	74	23
Summer									
Region									
Florida				2	5	8	1	7	1
Georgia	1	2	5	1	4	8	4	9	13
South Carolina	2	3	5	12	24	17	6	4	15
Long Bay				1	1	2	7	5	7
Onslow Bay	4	2	7	4	5	4	10	5	11
Raleigh Bay	4	2	3	7	4	9			
All areas	11	9	20	27	43	48	28	30	47
Autumn									
Region									
Florida				4	11	10	3	22	12
Georgia	9	18	18	7	17	17	5	11	12
South Carolina	7	12	6	9	20	19	7	11	8
Long Bay	1	2	1	6	7	9	12	14	8
Onslow Bay	15	20	25	5	3	7	1	8	2
Raleigh Bay	15	4	6	11	8	6	13	15	6
All areas	47	56	56	42	66	68	41	81	48
Total	65	82	81	103	155	152	108	185	118

Bony fishes, mostly bay anchovy (*Anchoa mitchilli*), striped anchovy (*A. hepsetus*), and other members of the class Actinopterygii, dominated the diet of weakfish, with a frequency of occurrence of 63% in stomachs that contained food (Table 2). The diet composition by weight consisted of 70% bony fishes. The highest diet component by number was nondecapod crustaceans (69%). In addition to bony fishes, the most frequently consumed prey items were mysids, the sergestid shrimp *Acetes americanus carolinae*, and various crustaceans. Values of mean percent weight and mean percent number predictably showed bony fishes to be the dominant prey consumed (44% and 35%, respectively); however, decapod crustaceans (32%) and nondecapod crustaceans (29%) had similarly high values for mean percent number (Fig. 2, A and B).

Results from the use of the Amundsen method indicate that the feeding strategy of weakfish was mixed because individuals sometimes chose specific prey but the population was often opportunistic with regard to what prey were selected. The top left portion of the graph in Figure 3A shows that many individuals chose specific prey types; however, the specific prey selected by each individual differed (Fig. 3A). The data points scattered throughout the center of this graph indicate a mixed feeding strategy, suggesting that, occasionally, the population would feed opportunistically.

Southern kingfish

Stomachs were processed for this study from 486 individuals, with an average size of 21 cm TL (for young-of-the-year fish through adult fish), and 422 of those stomachs contained food (86%; Table 1). Prey representing 86 taxa were identified (Table 2).

Decapod and nondecapod crustaceans were present in the majority of stomachs. Collected stomach sam-

Table 2

Frequency of prey occurrence (*%F*), diet composition by number (*%N*), diet composition by weight (%W), and index of relative importance expressed as a percent (IRI) of prey items found in stomachs of 3 predator species—weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*)—sampled off the Atlantic coast of the southeastern United States from 2008 through 2010.

	Weakfish				Southern kingfish				Atlantic croaker			
	%F	%N	%W	IRI	%F	%N	%W	IRI	%F	%N	%W	IRI
Bony fishes	62.7	7.4	70.27	4869.91	24.5	7.6	21.87	722.02	25.6	7.6	21	732.17
Actinopterygii	39.13	5.1	8.98	550.89	20.1	6.78	9.82	333.68	18.8	5.19	3.62	165.74
Anchoa hepsetus	10.51	0.96	30.1	326.35	0.25	0.09	0.38	0.12	1.42	0.21	8.99	13.11
Anchoa mitchilli	4.35	0.24	5.81	26.32	0.25	0.03	0.3	0.08	1.42	0.46	2.01	3.52
Anchoa spp.	4.35	0.36	3.85	18.3	1.23	0.3	1.19	1.82	2.85	0.88	4.37	14.96
Centropristis striata	1.45	0.08	2 73	4.07								
Clupeiformes	0.36	0.02	0.24	0.1								
Cynoscion nothus	1.45	0.1	2.54	3.82					0.28	0.04	0.79	0.24
Cynoscion spp.	2.17	0.16	1.86	4.39	0.49	0.06	0.35	0.2	1.14	0.17	0.81	1.11
Engraulidae	0.72	0.04	<.01	0.03	0.49	0.06	0.06	0.06	0.57	0.25	0.21	0.26
Harengula jaguana	0.36	0.02	0.23	0.09								
Larimus fasciatus	0.36	0.02	<.01	0.01								
Leiostomus xanthurus	2.54	0.18	9.17	23.72	0.25	0.03	0.27	0.07				
Ophichthidae					0.25	0.03	0.05	0.02				
Mugil cephalus	0.36	0.02	4.17	1.52								
Prionotus spp.	0.36	0.02	<.01	0.01	0.25	0.03	4.28	1.06				
Selene setapinnis					0.25	0.03	0.79	0.2				
Sciaenidae	0.36	0.02	0.01	0.01					0.85	0.38	0.2	0.49
Stellifer lanceolatus	1.09	0.06	0.59	0.7	0.49	0.06	0.21	0.13				
Symphurus plagiusa					0.25	0.03	3.49	0.86				
Syngnathus spp.					0.49	0.06	0.68	0.36				
Decapod crustaceans	54	23.1	20.52	2355.48	67.9	30.9	33.97	4404.99	45.3	18.8	21.53	1826.77
Acetes americanus carolinae	30.43	18.04	5.64	720.7	5.39	4.8	1.38	33.28	8.55	7.37	3.15	89.89
Albunea catherinae					0.49	0.06	0.76	0.4	0.28	0.04	0.26	0.09
Albuneidae					0.25	0.03	0.08	0.03	0.57	0.08	0.89	0.56
Axiidae									0.28	0.04	0.53	0.16
Brachyura	9.78	0.98	0.06	10.22	15.2	2.37	5.21	115.13	7.69	1.47	0.84	17.72
Callianassidae									0.85	0.21	0.09	0.25
Decapoda	1.45	0.1	0.07	0.24	4.9	0.98	0.57	7.59	2.85	0.71	0.1	2.33
Heterocrypta granulata					0.25	0.03	0.04	0.02	0.28	0.04	0.45	0.14
Latreutes parvulus					0.74	0.09	0.01	0.07	1.42	0.29	0.06	0.5
Leptochela sp.	5.8	0.64	0.21	4.93	12.5	3.26	0.83	51.11	7.41	1.38	0.38	13.07
Leucosiidae					0.74	0.09	0.25	0.25				
Lucifer faxoni	2.17	0.12	0.01	0.28	0.74	0.09	<.01	0.07	1.71	0.25	0.01	0.45
Ogyrides sp.	2.17	0.24	0.12	0.77	15.93	4.62	1.33	94.76	8.26	1.63	1.11	22.62
Paguroidea					3.43	0.44	2.52	10.19	3.7	0.59	1.58	8.04
Palaemonidae					0.98	0.12	0.01	0.12	0.85	0.13	0.01	0.12
Panopeidae					1.72	0.3	2.49	4.78	1.42	0.21	1.59	2.56
Pelia mutica	0.36	0.02	0	0.01								
Penaeidae	1.81	0.12	0.18	0.54	17.16	5.15	3.07	141.1	4.27	0.67	4.41	21.7
Pinnotheridae	3.26	0.26	0.1	1.16	9.07	1.69	1.34	27.46	4.27	1.05	0.5	6.61
Porcellanidae	1.81	0.1	0.01	0.19	0.49	0.12	0.6	0.35				
Portunidae	4.35	0.48	0.1	2.54	7.84	1.39	5.37	53.06	0.28	0.13	0.28	0.12
Rimapenaeus constrictus	11.23	1.57	5.6	80.52	14.71	5.21	7.6	188.46	5.98	2.13	1.93	24.32
Sicyonia laevigata					0.25	0.03	<.01	0.01				
Thalassinidea	2.17	0.36	5.87	13.54	0.49	0.06	0.49	0.27	1.42	0.25	1.93	3.11
Xanthoidea	0.36	0.02	<.01	0.01	0.25	0.03	0.02	0.01	0.85	0.13	1.42	1.33
Xiphopenaeus kroyeri	0.36	0.06	2.57	0.95								

Table continued

Table 2 (continued)

	Weakfish				Southern kingfish				Atlantic croaker			
	%F	%N	%W	IRI	%F	%N	%W	IRI	%F	%N	%W	IRI
Echinoderms					0.5	0.1	0.02	0.06	16.5	2.8	4.93	127.58
Echinoidea					0.49	0.06	0.02	0.04	0.57	0.08	0.01	0.05
Holothuroidea									1.99	0.67	1.29	3.91
Ophiuroidea									13.96	2.09	3.63	79.86
Mollusca	5.8	0.3	1.54	10.68	19.1	2.4	1.05	65.84	12.8	1.9	15.84	227.1
Arcidae									0.85	0.13	2.55	2.29
Bivalvia					4.9	0.62	9.97	51.91	4.84	0.71	4.21	23.83
Gastropoda									1.42	0.21	0.18	0.56
Mollusca	5.8	0.32	1.54	10.8	5.88	0.71	1.94	15.62	4.56	0.67	4.69	24.42
Solenidae					8.58	1.1	6.98	69.25	1.14	0.17	4.21	4.99
Nondecapod crustaceans	47.8	68.7	7.29	3632.32	62.3	41	14.73	3472.26	55.8	54.2	5.84	3350.01
Copepoda	8.33	6.26	0.12	53.18	0.74	0.65	0.01	0.48	7.12	7.37	0.08	53.03
Crustacea	18.12	1.1	1.87	53.89	12.5	2.4	1.13	44.06	20.8	4.02	2.6	137.58
Cumacea	2.54	2.63	0.01	6.69	18.87	10.48	0.31	203.76	5.13	1.63	0.06	8.67
Gammaridea	8.33	0.78	0.07	7.08	20.83	5.15	0.19	111.39	20.8	5.23	0.29	114.84
Isopoda	2.9	0.18	0.02	0.57	2.7	0.44	0.04	1.3	1.14	0.21	0.05	0.3
Mysidae	33.33	57.37	5.02	2079.4	35.05	21.23	1.19	785.77	25.64	35.5	2.59	976.51
Stomatopoda	4.35	0.34	0.2	2.34	4.9	0.68	11.87	61.51	1.42	0.21	0.17	0.54
Polychaetes	4.3	0.3	0.38	2.92	44.6	10	18.22	1258.49	51	12.1	28.95	2093.69
Ampharetidae	0.36	0.02	<.01	0.01	6.37	1.21	1.88	19.74	4.27	0.75	7.86	36.82
Aphroditidae					0.49	0.06	2.15	1.08				
Armandia agilis					7.11	1.72	0.37	14.86	4.56	0.96	0.43	6.36
Capitellidae					0.74	0.09	0.49	0.43	0.85	0.13	0.6	0.62
Cirratulidae									0.28	0.04	<.01	0.01
Glyceridae	1.09	0.06	0.06	0.13	3.92	0.47	0.98	5.71	3.7	0.54	3.04	13.26
Goniadidae					1.23	0.18	0.05	0.27	1.42	0.25	0.04	0.42
Lumbrineridae					1.47	0.18	1.27	2.13	0.85	0.13	0.3	0.36
Maldanidae					3.43	0.41	0.99	4.8	7.12	1.21	0.88	14.89
Nephtyidae					3.43	0.44	0.25	2.4	0.28	0.04	0.02	0.02
Nereididae					0.25	0.03	0.01	0.01	1.42	0.33	0.35	0.97
Oenonidae					1.47	0.18	0.08	0.38	2.56	0.38	0.5	2.25
Onuphidae	1.45	0.08	0.29	0.53	9.8	1.75	3.59	52.35	7.41	1.17	2.29	25.62
Opheliidae					0.74	0.09	0.02	0.08	3.13	0.54	0.46	3.16
Orbiniidae					0.49	0.06	0.03	0.04	3.42	0.54	0.18	2.48
Pectinariidae					0.49	0.06	0.19	0.12	0.85	0.13	2.83	2.52
Phyllodocidae					0.98	0.12	0.11	0.23	0.57	0.08	0.01	0.06
Polychaeta	1.45	0.14	0.03	0.24	11.03	1.45	2.18	40.03	16.52	2.43	6.11	141.1
Polynoidae									0.28	0.04	0.06	0.03
Sabellariidae					0.25	0.03	<.01	0.01	2.6	1.09	0.25	3.49
Sigalionidae					0.25	0.03	0.01	0.01	0.57	0.08	0.01	0.05
Spionidae					1.47	1.13	0.29	2.08	5.7	1	1.06	11.76
Terebellidae					2.21	0.36	3.26	7.97	0.57	0.08	0.04	0.07
Trichobranchidae									0.28	0.08	1.63	0.49
Other	0.4	0.2	<.01	0.08	4.2	7.5	1.06	35.95	1.7	0.4	0.19	1
Branchiostoma sp.					1.23	0.24	0.07	0.37				
Chaetognatha	0.36	0.18	<.01	0.07	0.98	6.9	0.13	6.89	0.57	0.17	0.01	0.1
Cnidaria					2.21	0.38	0.16	1.2	3.99	2.26	1.72	15.88
Echiura									0.28	0.04	0.14	0.05
Glottidia pyramidata					1.96	0.36	0.19	1.08	0.57	0.13	0.03	0.09
Sipuncula					0.25	0.03	0.67	0.17				
Tubificidae									0.28	0.08	0.01	0.03
Total		100	100			100	100			100	100	

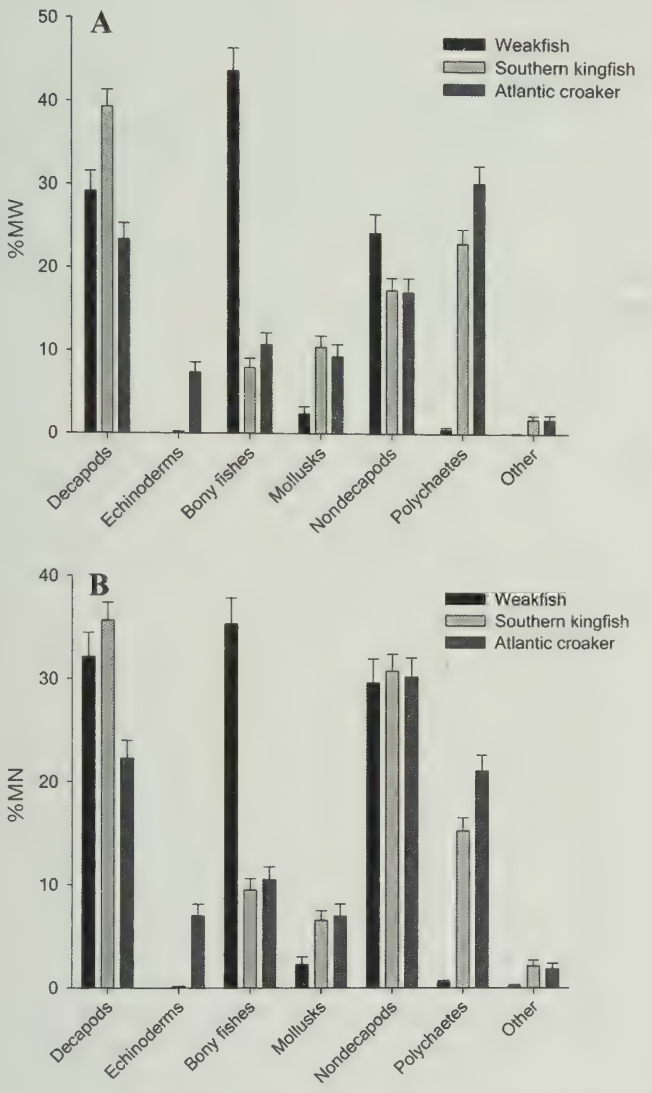

Figure 2

For weakfish (*Cynoscion regalis*; n=276), southern kingfish (*Menticirrhus americanus*; n=408), and Atlantic croaker (*Micropogonias undulatus*; n=351) captured in 2008, 2009, and 2010 off the Atlantic coast of the southeastern United States, (**A**) mean diet composition by weight (%MW) and (**B**) mean diet composition by number (%MN) by prey category: decapod crustaceans, echinoderms, bony fishes, mollusks, nondecapod crustaceans, polychaetes, and other (composed of unidentified animal tissue and rarely seen miscellaneous taxa). Error bars indicate 1 standard deviation of the mean.

ples contained decapod crustaceans 68% of the time and nondecapod crustaceans 62% of the time (Table 2). Polychaetes were identified in more than 40% of southern kingfish stomachs. Identified polychaetes included representatives from 20 different families, primarily Ampharetidae, Glyceridae, Nephtydae, Onuphidae, Opheliidae, and Terebellidae. Decapod crustaceans composed 33% of the composition by weight of the southern kingfish diet. Composition by number was higher for nondecapod crustaceans (41%) than for decapod crustaceans (31%). Mean percent weight and mean percent number were highest for decapod crustaceans (39% and 36%, respectively), compared with the mean values for all other prey categories. Polychaetes had the second-highest mean percent weight (23%), whereas nondecapod crustaceans represented 17% of the diet (Fig. 2, A and B).

Amundsen metrics indicate that the population of southern kingfish displayed a generalized feeding strategy. Although some prey items, including mysids, gammaridean amphipods, and cumaceans, were consumed regularly, most prey types were infrequently observed in the stomachs of southern kingfish (Fig. 3B). The concentration of data points along the y-axis in Figure 3B is indicative of prey items that were present in the stomachs of individual southern kingfish but were rarely if ever seen in the stomachs of more than a single animal.

Atlantic croaker

Of the 421 Atlantic croaker selected for diet analysis (with an average size of 18 cm TL for young-of-the-year fish through adult fish), 351 individuals had stomachs that contained prey items (83%; Table 1). Prey representing 91 taxa were identified (Table 2).

Nondecapod crustaceans (56%) and polychaetes (51%) were the prey categories with the highest frequencies of occurrence in the diet of Atlantic croaker in this study (Table 2). Decapod crustaceans (45%) were the third most frequent prey category. Values of composition by weight were comparable for bony fishes, decapods crustaceans, and polychaetes (21%, 22%, and 29%, respectively). Nondecapod crustaceans, most of which were mysids, had the highest value of composition by number (54%). Across all sampling years, polychaetes dominated mean percent weight, composing 30% of the prey weight (Fig. 2A). However, nondecapod crustaceans were numerically dominant, accounting for 30% of the number of prey (Fig. 2B).

Atlantic croaker were the most generalized feeders of the 3 sciaenids, according to the Amundsen plot in Figure 3C. Most of the data points in this figure appear along the y-axis, indicating that individual Atlantic croaker consumed many different prey types and that those prey types were rarely seen in the stomachs of other individual fish. The data points in the center of this graph indicate those prey that were more frequently found in the stomachs of Atlantic croaker than in the stomachs of the other 2 species: mysid shrimp, various unidentified crustacean parts, and gammaridean amphipods.

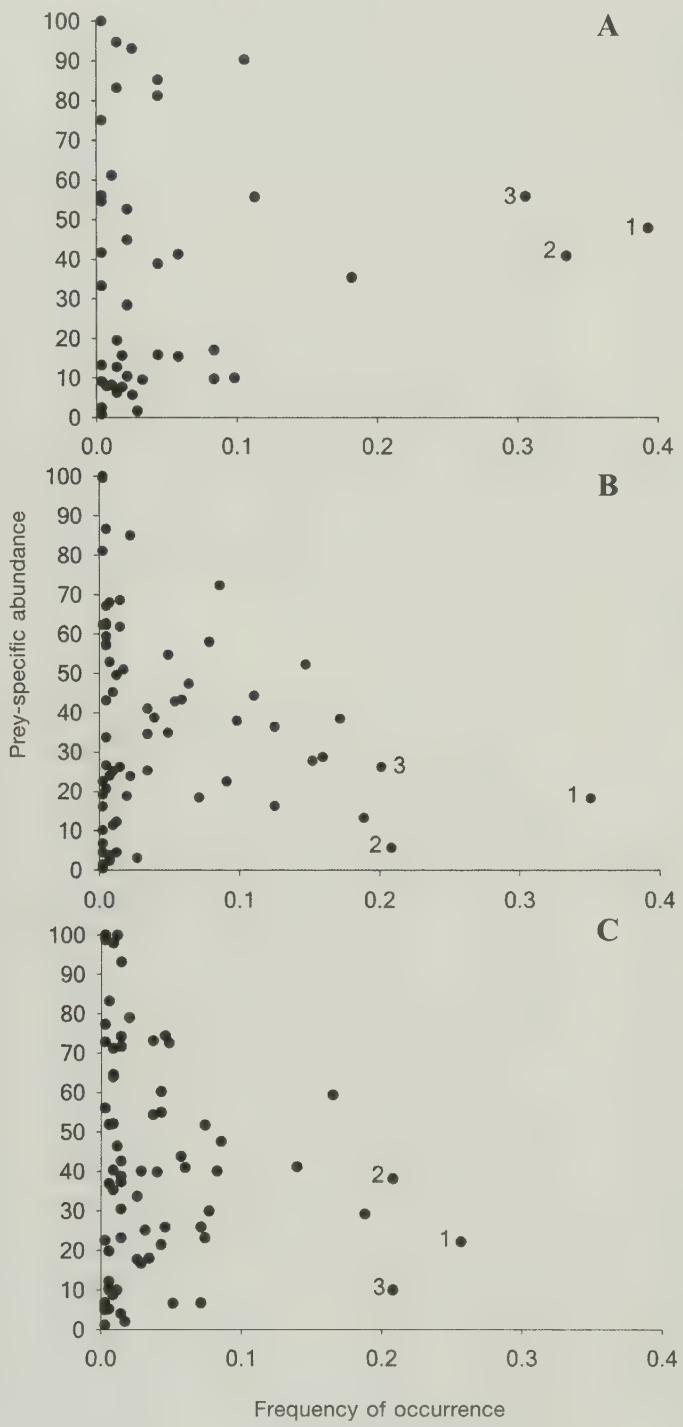

Figure 3

Plots of the feeding strategies of (**A**) weakfish (*Cynoscion regalis*), (**B**) southern kingfish (*Menticirrhus americanus*), and (**C**) Atlantic croaker (*Micropogonias undulatus*) determined with the Amundsen method. Prey consumed most frequently are numbered: 1=Actinopterygii, 2=Mysidae, and 3=*Acetes americanus carolinae* for weakfish; 1=Mysidae, 2=Gammaridea, and 3=Cumacea for southern kingfish; and 1=Mysidae, 2=Crustacea, and 3=Gammaridea for Atlantic croaker.

Overlap

The analysis performed on mean percent weight with the simplified M-H index indicates that some diet overlap was observed between species pairs (Table 3). The overlap was highest between southern kingfish and Atlantic croaker (M-H index=0.74; Table 3). M-H index for mean percent number indicated less diet overlap for all species pairs, although the overlap remained highest between southern kingfish and Atlantic croaker (M-H index=0.56).

Discussion

The diet of weakfish was distinct from that of the 2 other species examined; the most important prey consumed were bony fishes on the basis of both frequency of occurrence and composition by weight. Our findings are similar to those of Merriner (1975), who noted a diet dominated by bony fishes, particularly anchovies and the larger Atlantic thread herring, by occurrence, number, and volume. In contrast to Merriner (1975), we did not specifically identify any Atlantic thread herring in the weakfish stomachs. It is possible that the clupeid Atlantic thread herring was present , but our fish remains were identified only to family. Species of *Anchoa*, mostly striped anchovy and bay anchovy, were observed in 19% of stomachs compared with 58% of stomachs in Merriner's study. Again, it is feasible that species of *Anchoa* were present in a higher percentage of stomachs, but identification of fishes was difficult because specimens were often highly digested.

Although the composition by number indicates that nondecapod crustaceans played an important role in the diet of weakfish (57% of total prey composition by number), this finding may be misleading. Mysids are quite small and known to occur in aggregations (Omori and Hamner, 1982). It is very possible that the high numerical occurrence that we found is the result of opportunistic encounters with mysid patches rather than an indication of targeted prey selection or high nutritional importance in weakfish diets. Bony fishes were the largest dietary component by weight, and weight is a more relevant measurement of energetic importance of organisms in fish diets than is number (Bowen, 1983; Chipps and Garvey, 2007).

The diet of southern kingfish is similar across the range of this species and includes polychaetes, amphipods, and mysids. However, the frequency of occurrence of various prey items differs with location. Off the southeastern United States, we found that various taxa of crustaceans were the most important prey

Table 3

Results from the simplified Morisita-Horn index used for analysis of diet overlap for pairs of 3 species: weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*). An asterisk (*) denotes a value that indicates biologically significant potential for diet overlap between species in a pair. Analyses were performed for both mean percent weight (%MW) and mean percent number (%MN).

Predator cross pairs	Weakfish and southern kingfish	Southern kingfish and Atlantic croaker	Atlantic croaker and weakfish
%MW	0.46	0.74*	0.50
%MN	0.40	0.56	0.43

items according to all 3 of the diet metrics analyzed (frequency of occurrence, composition by number, and composition by weight). Polychaetes were also important, occurring in nearly half of the stomachs for all years of this study, compared with polychaetes ranking fourth in the diet of southern kingfish in a study in the Gulf of Mexico (McMichael and Ross, 1987). Clam siphons were the most frequently occurring prey item in our study, but, in another study in Brazil, amphipods were the most common prey item in spring, followed by polychaetes and mysids (Rodrigues and Vieira, 2010). The Gulf of Mexico and Brazilian study defined juvenile fishes as those ranging in TL between 2 and 6 cm, but few fishes less than 10 cm TL were observed in our study. A possible explanation for the differences in diet are ontogenetic changes in foraging behavior and swimming ability that, in turn, increase foraging areas and feeding opportunities for larger fishes (Graham et al., 2007).

The diet of Atlantic croaker was the most diverse of among the diets of the 3 sciaenids and our findings are comparable with those of Overstreet and Heard's (1978) study of this species in the Gulf of Mexico. The diet patterns that we observed are most similar to those of Atlantic croaker captured in nearshore waters, at depths consistent with the depth range of our sampling. Statistical analyses indicated no seasonal shift in diet in either our study or in that of Overstreet and Heard (1978), but we found that the diet of Atlantic croaker included a markedly higher frequency of occurrence for echinoderms, specifically ophiuroids, which were present in an average of 16% of stomachs, compared with <4% of the stomachs in the Gulf of Mexico study (Overstreet and Heard, 1978). This difference could be a result of variance in the distribution of ophiuroids, which are quite common off the southeastern coast of the United States, or may be the result of other prey types being more readily available to Atlantic croaker populations in the Gulf of Mexico.

Foraging habitats and feeding strategy varied among the 3 species in this study. Southern kingfish and Atlantic croaker consumed prey that are associated with the seafloor, whereas weakfish generally fed on prey items that occur in the water column. Furthermore, southern kingfish and Atlantic croaker can be characterized as having a more generalized feeding strategy. Despite the variation in feeding strategy, a few prey items were consumed by all 3 species, such as the amphipods *Erichthonius brasiliensis* and *Microprotopus raneyi* and the mysid *Promysis atlantica.* Mysids were the most frequently consumed individual prey item for both southern kingfish and Atlantic croaker, and the second-most frequently consumed individual prey item of weakfish. Some animals, such as most mysid species, exhibit diel vertical migrations, spending daylight hours on the seafloor and migrating toward the surface at dusk to forage throughout the night or vice versa (Robertson and Howard, 1978). These vertical migration patterns provide an opportunity for predatory fishes to encounter and consume prey that may only temporarily dwell in their foraging habitat (Goldman and Sedberry, 2010), therefore, creating an opportunity for diet overlap between bottom-feeding fishes and water-column–feeding fishes.

The 3 species examined here did not exclusively employ a single feeding strategy (e.g., generalist or specialist). Individuals of all 3 species consumed specific prey items, but, at the population level, each species showed a proclivity to feed opportunistically—a finding that could be interpreted as indicating that they fed on whatever was both available and abundant. In comparison with the populations of the other 2 fish species, the weakfish population showed a trend toward more specialized feeding, shifting to more mobile, pelagic prey earlier in their ontogeny. Weakfish also have the potential to reach the greatest size, and changes in their diet as they grow would be expected to reduce diet overlap with species that have a smaller terminal size (Schoener, 1974; Werner and Gilliam, 1984). Alternatively, the morphological features of the 3 species indicates that weakfish would be more likely to feed in

the water column than the other 2 species, regardless of body size.

The highest potential for resource competition exists between southern kingfish and Atlantic croaker on the basis of the simplified M-H index. Morisita-Horn index values exceeding 0.60 are generally accepted as biologically significant in the literature (Zaret and Rand, 1971; Labropoulou and Eleftheriou, 1997; King and Beamish, 2000; Graham et al., 2007; Rodrigues and Vieira, 2010). Assuming this value is significant, southern kingfish and Atlantic croaker showed significant diet overlap by mean percent weight, at 0.74, but not on the basis of mean percent number, at 0.56 (Table 3). Most southern kingfish and Atlantic croaker that were sampled had prey in their stomachs, indicating that sufficient prey were readily available to both species and the generalized (opportunistic) feeding strategy employed by these benthivorous species likely reduces any competition for resources, even when there are relatively high levels of diet overlap.

Ecosystem-based management is dependent on defining interactions among species and, in particular, on identifying trophic links for priority species (NMFS[6]). Weakfish, southern kingfish, and Atlantic croaker are swept up regularly in commercial shrimp trawl nets, are targets of bait fisheries, and play important roles in the nearshore food web. If exploitation increases, their large-scale removal could alter some fundamental ecosystem processes (Kumar and Deepthi, 2006). The sciaenids in this study overlap spatially; therefore, ecosystem-based principles require that we determine whether competitive interactions occur among them for prey resources. Ignorance of predator–prey relationships will result in fisheries managers overlooking important ecosystem-based complexities that could drive population trends (Ruckelshaus, 2008).

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[6] NMFS (National Marine Fisheries Service). 1999. Ecosystem-based fishery management: a report to Congress by the Ecosystem Principles Advisory Panel, 46 p. [Available at website, accessed August 2014.]

Literature cited

Ainsworth, C. H., D. A. Varkey, and T. J. Pitcher.
2008. Ecosystem simulation models of Raja Ampat, Indonesia, in support of ecosystem-based fisheries management. *In* Ecological and economic analyses of marine ecosystems in the Bird's Head seascape, Papau, Indonesia: II (M. Bailey and T. J. Pitcher, eds.). Fish. Cent. Res. Rep. 16(1):3–124. [Available at website.]

Amundsen P.-A., H.-M. Gabler, and F. J. Staldvik.
1996. A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. J. Fish Biol. 48:607–614.

Barbieri L. R., M. E. Chittenden Jr., and S. K. Lowerre-Barbieri.
1994. Maturity, spawning, and ovarian cycle of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters. Fish. Bull. 92:671–685.

Bearden, C. W.
1963. A contribution to the biology of the king whitings, genus *Menticirrhus*, of South Carolina. Contrib. Bears Bluff Lab. 38, 27 p.

Bowen, S. H.
1983. Quantitative description of the diet. *In* Fisheries techniques (L. A. Nielsen and D. L. Johnson, eds.), p. 325–336. Am. Fish. Soc., Bethesda, MD.

Bozzetti, M., and U. H. Schulz.
2004. An index of biotic integrity based on fish assemblages for subtropical streams in southern Brazil. Hydrobiologia 529:133–144.

Brodziak, J., and J. Link.
2002. Ecosystem-based fishery management: what is it and how can we do it? Bull. Mar. Sci. 70:589–611.

Chao, N. L.
2002. Sciaenidae. *In* The living marine resources of the Western Central Atlantic, vol. III: bony fishes part 2 (Opistognathidae to Molidae), sea turtles and marine mammals (K. E. Carpenter, ed.), 1583–1653 p. FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5. FAO, Rome.

Chipps, S. R., and J. E. Garvey.
2007. Assessment of diets and feeding patterns. *In* Analysis and interpretation of freshwater fisheries data (C. S. Guy and M. L. Brown, eds.), p. 473–514. Am. Fish. Soc., Bethesda, MD.

Cortés, E.
1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can. J. Fish Aquat. Sci. 54:726–738.

Costello, M. J.
1990. Predator feeding strategy and prey importance: a new graphical analysis. J. Fish Biol. 36: 261–263.

Diamond, S. L., L. G. Cowell, and L. B. Crowder.
2000. Population effects of shrimp trawl bycatch on Atlantic croaker. Can. J. Fish. Aquat. Sci. 57: 2010–2021.

Goldman, S. F., and G. R. Sedberry.
2010. Feeding habits of some demersal fish on the Charleston Bump off the southeastern United States. ICES J. Mar. Sci. 68:390–398.

Goode, G. B. (ed.)
1884. The fisheries and fishery industry of the United States, vol. 1, 808 p. Government Printing Office, Washington, D.C.

Graham, B. S., D. Grubbs, K. Holland, and B. N. Popp.
2007. A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. Mar. Biol. 150:647–658.

Hales, L. S., Jr., and E. J. Reitz.
1992. Historical changes in age and growth of Atlantic croaker, *Micropogonias undulatus* (Perciformes: Sciaenidae). J. Archaeol. Sci. 19:73–99.

Hansson, S.
1998. Methods of studying fish feeding: a comment. Can. J. Fish. Aquat. Sci. 55:2706–2707.

Harding, S. M., and M. E. Chittenden Jr.
1987. Reproduction, movements and population dynamics of the southern kingfish, *Menticirrhus americanus*, in the northwestern Gulf of Mexico. NOAA Tech. Rep. NMFS 49, 21 p.

Hyslop, E. J.
1980. Stomach contents analysis—a review of methods and their application. J. Fish Biol. 17:411–429.

King, J. R., and R. J. Beamish.
2000. Diet comparisons indicate a competitive interaction between ocean age-0 chum and coho salmon. NPAFC Bull. 2:65–74. [Available at website.]

Kumar, A. B., and G. R. Deepthi.
2006. Trawling and by-catch: implications on marine ecosystem. Curr. Sci. 90: 922–931. [Available at website.]

Labropoulou, M., and A. Eleftheriou.
1997. The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. J. Fish Biol. 50:324–340.

Link, J. S.
2002. What does ecosystem-based fisheries management mean? Fisheries 27(4):18–21.

Magnuson-Stevens Fishery Conservation and Management Reauthorization Act of 2006.
2007. 16 U.S.C. 1881c (2007). [Available at website.]

McCune, B., and J. B. Grace.
2002. Analysis of ecological communities, 304 p. MjM Software Design, Gleneden Beach, OR.

McMichael, R. H., Jr., and S. T. Ross.
1987. The relative abundance and feeding habits of juvenile kingfish (Sciaenidae: *Menticirrhus*) in a Gulf of Mexico surf zone. NE Gulf Sci. 9:109–123.

Merriner, J. V.
1975. Food habits of the weakfish, *Cynoscion regalis*, in North Carolina waters. Chesapeake Sci. 16:74–76.

Murray, J. D., J. J. Bahen, and R. A. Rulifson.
1992. Management considerations for by-catch in the North Carolina and Southeast Shrimp Fishery. Fisheries 17(1):21–26.

Musick, J. A., and M. L. Wiley.
1972. Fishes of the Chesapeake Bay. Chesapeake Sci. 13:S121–S122.

Omori, M., and W. M. Hamner.
1982. Patchy distribution of zooplankton: behavior, population assessment and sampling problems. Mar. Biol. 72:193–200.

Overstreet, R. M., and R. W. Heard.
1978. Food of the Atlantic croaker, *Micropogonias undulatus*, from Mississippi Sound and the Gulf of Mexico. Gulf. Res. Rep. 6:145–152..

Pinkas, L., M. S. Oliphant, and I. L. K. Iverson.
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152, 105 p. [Available at website, accessed December 2014].

R Core Team.
2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from website, accessed November 2012.]

Robertson, A. I., and R. K. Howard.
1978. Diel trophic interactions between vertically-migrating zooplankton and their fish predators in an eelgrass community. Mar. Biol. 48:207–213.

Rodrigues, F. L., and J. P. Vieira.
2010. Feeding strategy of *Menticirrhus americanus* and *Menticirrhus littoralis* (Perciformes: Sciaenidae) juveniles in a sandy beach surf zone of southern Brazil. Zoologia 27:873–880.

Ross, S. W.
1988. Age, growth, and mortality of Atlantic croaker in North Carolina, with comments on population dynamics. Trans. Am. Fish. Soc. 117:461–473.

Ruckelshaus, M., T. Klinger, N. Knowlton, and D. P. DeMaster.
2008. Marine ecosystem-based management in practice: scientific and governance challenges. BioScience 58:53–63.

Schoener, T. W.
1974. Resource partitioning in ecological communities. Science 185:27–39.

Shepherd, G., and B. Grimes.
1983. Geographic and historic variations in growth of weakfish, *Cynoscion regalis*, in the Middle Atlantic Bight. Fish. Bull. 81:803–813.

Smith, J. W., and C. A. Wenner.
1985. Biology of the southern kingfish in the South Atlantic Bight. Trans. Am. Fish. Soc. 114:356–366.

Walton, C.
1996. Age, growth and reproductive seasonality of the weakfish, *Cynoscion regalis*, along the southeast Atlantic coast of the United States. M.S. thesis, 85 p. Coll. Charleston, Charleston, SC.

Werner, E. E., and J. F. Gilliam.
1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15:393–425.

Wolda, H.
1981. Similarity indices, sample size and diversity. Oecologia 50:296–302.

Zaret, T. M., and A. S. Rand.
1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:2:336–342.

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Sensitivity of yield-per-recruit and spawning-biomass-per-recruit models to bias and imprecision in life history parameters: an example based on life history parameters of Japanese eel (*Anguilla japonica*)

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Abstract—Yield-per-recruit and spawning-biomass-per-recruit models, are commonly used for evaluating the status of a fishery. In practice, model parameters are themselves usually estimates that are subject to both bias (uncertainty in the mean) and imprecision (uncertainty in the standard deviation). Using Monte Carlo simulation with data for female Japanese eel (*Anguilla japonica*) from the Kao-Ping River in Taiwan, we examined the sensitivity of such models to different degrees of bias and imprecision in the life history parameters. Positive biases in natural mortality and the von Bertalanffy growth coefficient led to larger relative changes in the mean and standard deviation of estimated fishing-mortality–based biological reference points (F_{BRPs}) than did changes under negative biases. Higher degrees of imprecision in parameters did not affect the means of F_{BRPs}, but their standard deviations increased. Composite risks of overfishing depended mainly on the changes in the means of F_{BRPs} rather than on their standard deviations. Therefore, reducing the biases in key life history parameters, as well as the bias and imprecision in the current rate of fishing mortality, may be the most relevant approach for obtaining correct estimates of the risks of overfishing.

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Yield-per-recruit (YPR) and spawning-biomass-per-recruit (SPR) models, in which the total yield or spawning biomass of a cohort is standardized for the numbers of recruits, are commonly used in fisheries assessment (Beverton and Holt, 1957; Quinn and Deriso, 1999). They can be used to infer the total yield and spawning biomass of an entire population composed of different cohorts with an assumption of a steady state and with knowledge of equilibrium recruitment (King, 2007). Several fishing-mortality–based biological reference points (F_{BRPs}) derived from YPR and SPR models can be used to evaluate whether the yield per recruit is optimal or the spawning biomass per recruit is sufficient for the population to persist under current fishing pressure.

Uncertainties in the parameters of such models are inevitable and result from observation and process error (Charles, 1998). Ignoring uncertainties in parameters can lead to incorrect estimation of F_{BRPs}, and consequently the examination of fishery status could be misleading, given the cases of the American lobster (*Homarus americanus*) (Chen and Wilson, 2002), green sea urchin (*Strongylocentrotus droebachiensis*) (Grabowski and Chen, 2004), Atlantic cod (*Gadus morhua*) (Jiao et al., 2005), pronghorn spiny lobster (*Panulirus penicillatus*) (Chang et al., 2009), and Japanese eel (*Anguilla japonica*) (Lin et al., 2010a).

Estimation of natural mortality (M) is challenging (Vetter, 1988) because both its mean and variance are prone to considerable uncertainty. For example, the estimates of M have varied among different empirical methods (Pascual and Iribarne, 1993; Lin and Sun, 2013). The variances of M estimates also have differed among approaches (e.g., Cubillos et al., 1999, versus Hall et al., 2004; Lin et al., 2012). It is easier to obtain growth information. The von Bertalanffy growth function is an

often used growth model, but different estimation approaches (e.g., length-frequency methods versus readings of rings in calcified structures; see Lin and Tzeng, 2009, versus Lin and Tzeng, 2010), different regions of study (Helser and Lai, 2004; Keller et al., 2012), and aging errors from annuli readings (Lai and Gunderson, 1987; Cope and Punt, 2007) may lead to biases in the von Bertalanffy growth coefficient (K).

In another example of the potential for uncertainty, biases in the asymptotic length (L_∞) may result from the regional variation in growth potential in different habitats (Beverton and Holt, 1957), from a latitudinal trend (Helser and Lai, 2004; Keller et al., 2012), or from sampling schemes unrepresentative of the population size structure, because of its high dependency of maximum size in the sample (Formacion et al., 1991; Froese and Binohlan, 2000). In addition, the uncertainty (or multiplicative error) in the growth curve (ε_{GR}) is related to the imprecision in the lengths-at-age scatter at a given age. The current fishing mortality rate (F_{cur}) can be estimated from various methods (e.g., Seber, 1982; Quinn and Deriso, 1999; King, 2007) with both the mean and variance of high uncertainty (Chen and Wilson, 2002).

It is essential to incorporate and quantify these uncertainties in the assessment of population dynamics (Hilborn and Walters, 1992; Peterman, 2004). Further, parameter uncertainties can be categorized into bias uncertainty and precision uncertainty. The influence of parameter bias on YPR and SPR models has been investigated since the 1950s (e.g., Beverton and Holt, 1957; Goodyear, 1993; Mace, 1994), but the effects of precision uncertainty have seldom been addressed. The effects of parameter imprecision with a limited number of comparisons (i.e., high or low variation) that were inadequate to reveal a full picture of the sensitivity to bias and imprecision in the parameters have been examined in a few studies (e.g., Restrepo and Fox, 1988; Chen and Wilson, 2002; Chang et al., 2009). Systematic examinations of different degrees of parameter bias and imprecision with a wider range and finer resolution could provide detailed information about their effects on model outputs (e.g., Goodyear, 1993), but few such examinations exist for per-recruit models.

It is difficult to elucidate the sensitivity of per-recruit models to parameter bias and imprecision through analysis of the formulae because the effects of the parameters on F_{BRPs} are nonlinear with complicated forms (Schnute and Richard, 1998). Alternatively, a sensitivity analysis through the use of a Monte Carlo simulation can be used to examine their effects on the estimation of F_{BRPs}, on fishery status, and on management implications (Jiao et al., 2005). Therefore, the objective of this study was to evaluate the effects of different degrees of bias, represented by the differences in parameter means, and of imprecision, represented by the differences in parameter standard deviations (SDs), in the YPR and SPR model results, specifically in the F_{BRPs} and the resultant composite risks of overfishing.

Materials and methods

To better understand the sensitivity of outputs from the YPR and SPR models, we changed the mean or SD of selected parameters one at a time over large ranges with fine increments (from 5% to 95% with increments of 5% for cases of under-specification and from 150% to 1000% with increments of 50% for cases of over-specification). The following parameters were selected: 1) M; 2) von Bertalanffy growth coefficients of K and L_∞; and 3) F_{cur}. In addition, the multiplicative error in the growth curve (ε_{GR}) and length–weight relationship (ε_{LW}) were selected as well. In this study, we used information on the mean and SD values of these parameters from previous studies conducted during 1998–2006 on the life history and fishery of the Japanese eel in the Kao-Ping River in Taiwan (Lin and Tzeng 2009; Lin et al. 2010a, 2010b) to examine the sensitivity of model results to effects of parameter bias and imprecision with a Monte Carlo simulation.

We used wide ranges for the parameters for 3 reasons: 1) the scale of boundaries used; a factor of 10 was applied in a classical study (figure 4 in Goodyear, 1993); 2) a wide range is more general because it can include all likely ranges; and 3) in our previous study (Lin and Sun, 2013), we found that the variation in estimates of M from several different indirect methods can vary from 0.10/year to 2.13/year. Also, the difference in K can be large, especially when different approaches are involved. For the same region, for example, in Kao-Ping River, K has varied from 0.12/year to 0.38/year, depending on whether methods based on otoliths or length frequencies were applied (Lin and Tzeng, 2009, 2010).

YPR and SPR models

The YPR and SPR models were calculated according to the formulae in Quinn and Deriso (1999):

$$YPR = e^{-M(t_c - t_r)} \int_{t_c}^{t_{max}} F(t)N(t)W(t)dt \quad \text{and} \qquad (1)$$

$$SPR = \int_{t_c}^{t_{max}} N(t)W(t)S(t)dt, \qquad (2)$$

where $F(t)$ = the fishing mortality at age t;
$N(t)$ = population size in numbers at age t;
$W(t)$ = the weight at age t;
$S(t)$ = the maturation proportion at age t;
t_r = the age at recruitment;
t_c = the age at first capture; and
t_{max} = the maximum age (the formulae for $F(t)$, $N(t)$, $W(t)$, and $S(t)$ are shown in Table 1).

Because, in Kao-Ping River, females were 4 times more abundant than males (Han and Tzeng, 2006) and because females contribute more directly to spawning biomass, the parameters of female Japanese eels were used in this study; they were also used in Lin et al. (2010a). Estimates of means and corresponding SDs of the parameters were derived from our previous works (Lin and Tzeng, 2009; Lin et al.,2010b).

Table 1

Formulae, estimates of model parameters, and corresponding simulated random errors for the length–weight relationship (a and b are coefficients, and ε_{LW}=the corresponding multiplicative error), N=the population size in numbers; von Bertalanffy growth function (K=the growth coefficient (/year), L_∞=the asymptotic length (mm), t_0=the theoretical age at length of zero (year), and ε_{GR}=the multiplicative error of the growth curve), M=the natural mortality (/year); ε_M=the standard deviation of M; F_{cur}=current fishing mortality (/year); fishing process under gear selection (α_0 and α_1=selection curve coefficients), and maturation process of female Japanese eel (*Anguilla japonica*) in the lower reach of the Kao-Ping River in southern Taiwan (β_0 and β_1=the maturation curve coefficients, and $\varepsilon_{\beta 0}$ and $\varepsilon_{\beta 1}$=the standard error for β_0 and β_1, respectively). The means and standard deviations of the parameters are from previous studies conducted in 1998–2006 on life history parameters and the fishery of Japanese eel in the Kao-Ping River, Taiwan (Lin and Tzeng 2009, Lin et al. 2010a, 2010b).

Formula	Parameter
Weight at age t, $W(t)$	
$W(t) = aL(t)^b e^{\varepsilon_{LW}}$	$a, b = 4.56 \times 10^{-8}, 3.55$
	$\varepsilon_{LW} \sim N(0, 3.93 \times 10^{-4})$
$L(t) = L_\infty[1 - e^{-K(t-t_0)}]e^{\varepsilon_{GR}}$	$L_\infty, K, t_0 = 1024, 0.12, -0.69$
	$\varepsilon_{GR} \sim N(0, 3.10 \times 10^{-2})$
Population size in number at age t, $N(t)$	
$N(t) = e^{-[F(t)+(M+\varepsilon_M)](t-t_r)}$	$M = 0.18$/year
	$\varepsilon_M \sim N(0, 1.98 \times 10^{-5})$
Fishing process under logistic gear selection, $F(t)$	
$F(t) = F_{cur} \times \frac{e[\alpha_0 + \alpha_1 L(t)]}{1 + e[\alpha_0 + \alpha_1 L(t)]}$	$F_{cur} \sim$ *Gamma* with mean of 0.12 and variance of 1.06×10^{-2}, $\alpha_0, \alpha_1 = -4, 0.02$
Maturation (silvering) proportion at age t, $S(t)$	
$S(t) = \frac{e^{[(\beta_0+\varepsilon_{\beta_0})+(\beta_1+\varepsilon_{\beta_1})L(t)]}}{1 + e^{[(\beta_0+\varepsilon_{\beta_0})+(\beta_1+\varepsilon_{\beta_1})L(t)]}}$	$\beta_0, \beta_1 = -13.31, 0.02$
	$\varepsilon_{\beta_0} \sim N(0, 1.36)$ and
	$\varepsilon_{\beta_1} \sim N(0, 4.04 \times 10^{-6})$
Others	
Maximum observed age, t_{max}	16 years
Length and age at recruitment, L_r, t_r	55 mm, 0.489 year
Length and age at first capture, L_c, t_c	200 mm, 1.15 year

Four F_{BRPs} were calculated to compare with F_{cur}(0.120/year, Lin et al., 2010b): F_{max}, the fishing mortality at which yield per recruit is at its maximum; $F_{0.1}$, the fishing mortality at which the increase of yield per recruit is only 10% of the increase of yield per recruit when fishing mortality is zero (King, 2007); and $F_{30\%}$ and $F_{50\%}$, the fishing mortality rates at which the SPR is 30% and 50% of the SPR when fishing mortality is zero (Goodyear, 1993).

The reference points F_{max} and $F_{0.1}$ can be regarded as boundaries in order to constrain harvesting below the level within which the fish population can produce maximum sustainable yield (United Nations, 1995), and they usually are used as limiting and precautionary indicators of growth overfishing, respectively; fishing mortality rates above F_{max} indicate that fish are caught before they reach optimal size given the rate of natural mortality and their growth rate (Gabriel and Mace, 1999; Quinn and Deriso, 1999). Fishing mortalities at 30% and 50% of SPR, compared with SPR at F=0, are considered to be the limiting and precautionary levels for anguillid eels (ICES[1]). Therefore, $F_{30\%}$ and $F_{50\%}$ were considered the limiting and precautionary reference points for recruitment overfishing, where the spawners are insufficient in numbers to produce enough offspring to replace themselves (Sissenwine and Shepherd, 1987).

Incorporation of uncertainties in parameters

We used Monte Carlo simulation, which has been widely applied to other species (e.g., Chen and Wilson, 2002; Grabowski and Chen, 2004; Chang et al., 2009; Lin et al., 2010a) to incorporate the uncertainties of the parameters into the models. In each run, random errors for natural mortality (ε_M) and for coefficients in the logistic maturation curve (ε_{β_0} and ε_{β_1}), as well as ε_{LW}

[1] ICES (International Council for the Exploration of the Sea). 2002. Report of the ICES/EIFAC Working Group on Eels. ICES Council Meeting (C.M.) Documents 2002/ACFM:03, 55 p. [Available at website.]

Table 2

Summary of the 9 scenarios for evaluation of the sensitivity of the results from models of yield per recruit and spawning biomass per recruit to different degrees of bias and imprecision in several parameters: natural mortality (M), von Bertalanffy growth coefficient (K), asymptotic length (L_∞), and current fishing mortality rate (F_{cur}). Also the multiplicative error in the growth curve (ε_{GR}) and the length–weight (LW) relationship (ε_{LW}) are modeled. In each scenario, the mean or standard deviation (SD) of only one parameter was changed.

Scenario	Description	Parameter	Range
1	Standard scenario	Unchanged	100%
2	Mean of M	M	10–1000%
3	SD of M	ε_M	10–1000%
4	Mean of K	K	10–1000%
5	Mean of L_∞	L_∞	50–200%
6	Error in growth curve	ε_{GR}	10–1000%
7	Error in LW relationship	ε_{LW}	10–1000%
8	Mean of F_{cur}	F_{cur}	10–1000%
9	SD of F_{cur}	ε_{Fcur}	10–1000%

and ε_{GR}, were generated from normal distribution with the means and variances listed in Table 1. These random errors were incorporated into the YPR and SPR formulae provided in Table 1, and then 4 F_{BRP}s (F_{max}, $F_{0.1}$, $F_{30\%}$, and $F_{50\%}$) were calculated. For each simulation scenario, this process was repeated 5000 times to produce 5000 corresponding sets of F_{BRP} values from which the empirical distributions of the 4 F_{BRP}s were generated and composite risks were calculated.

Calculation of composite risks

Because F_{cur} and the F_{BRP}s are not fixed constants, we applied composite risk analysis that allowed for the incorporation of the uncertainty in both indicator and management reference points (Prager et al., 2003; Jiao et al., 2005). By the discrete approach proposed by Jiao et al. (2005), the composite risks were calculated as the expected probability of one random variable being larger than another. Let $f(x)$ be the empirical probability density function of the F_{BRP} of interest (e.g., F_{max}) and $g(y)$ be the empirical probability density function of F_{cur} with a corresponding cumulative density function of $G(y)$ and then, let Δx be a small increase in x (i.e., the F_{BRP}), and by summing x over its range, the composite risk of F_{cur} exceeding F_{BRP} is calculated with the following equation:

$$P(F_{cur} > F_{BRP} = 1 - \sum_{-\infty}^{\infty} [G(x)f(x)]\Delta x \qquad (3)$$

Here, we assume a gamma distribution for F_{cur} because 1) our previous study (Lin and Tzeng, 2008) indicated that gamma distribution fitted better for the distribution of fishing efforts, 2) it produces nonnegative values, and 3) it is flexible in shape. For details in calculation of composite risks in discrete approach, refer to Jiao et al. (2005).

Sensitivity analysis

For the sensitivity analysis, the parameter values in Table 1 were set as the standard scenario (scenario 1; Table 2). The parameters for which mean and SD values may potentially affect results of YPR and SPR models were investigated in 9 scenarios, in which the mean or SD of only one parameter was changed (Table 2): the mean of M (scenario 2) and its SD (ε_M, scenario 3), the mean of K (scenario 4), and the mean of L_∞ (scenario 5). In practice, the bias in K can result from aging error and the use of different estimation approaches, and the bias in L_∞ often results from unrepresentative sampling schemes. Therefore, we assumed that the sources of biases in K and L_∞ are unrelatedand they were modeled independently. Because modeling the estimation errors in the coefficients K and L_∞ can lead to underestimation of the actual uncertainty in the data (Lin et al., 2012), the error was modeled on the growth curve (ε_{GR}) rather than coefficients (scenario 6). The remaining scenarios are ε_{LW} (scenario 7) and the mean and SD values of F_{cur} and ε_{Fcur} (scenarios 8 and 9).

For scenarios 1–7, the mean and SD values of the parameters, except for L_∞, were decreased to 10% with an increment of 5% or were increased to 1000% with an increment of 50% to cover the possible magnitudes of biological variation (as applied in Goodyear, 1993). Because information about L_∞ can be obtained from the maximum observed length in the data, that parameter may be subject to less bias and imprecision and was set from 50% to 100% with an increment of 5% and from 100% to 200% with an increment of 10% (Table 2). For scenarios 8 and 9, because of less computational load (calculation of an F_{BRP} is independent of F_{cur}, and, therefore, we needed to compute only composite risks of overfishing), we used finer increments: the mean and SD of F_{cur} were decreased to 10% with an increment of 1% or increased to 1000% with an increment of 10%.

The relative change (RC) between the mean or SD of one F_{BRP} for increment i in scenario j ($RC^{ij}_{F_{BRP}}$) and the mean or SD of that F_{BRP} in the standard scenario was used to quantify the sensitivity of a given F_{BRP} for all scenarios except 8 and 9. RC is defined with the following equation:

$$RC^{ij}_{F_{BRP}} = 100 \times T^{ij}_{F_{BRP}} \times (T^{S}_{F_{BRP}})^{-1}, \qquad (4)$$

Where $T^{ij}_{F_{BRP}}$ = the statistic (mean or SD) of the F_{BRP} of interest (e.g., F_{max}) for increment i in scenario j; and

Table 3

Mean and standard deviation (SD) per year of 4 fishery-mortality–based reference points(F_{BRPs})—the fishing mortality at which yield per recruit is at its maximum (F_{max}),the fishing mortality at which the increase of yield per recruit is only 10% of the increase of yield per recruit when fishing mortality is zero($F_{0.1}$), and the fishing mortality rates at which the spawning biomass per recruit (SPR) is 30% and 50% of the SPR when fishing mortality is zero($F_{30\%}$and $F_{50\%}$)—and the composite risks, $P(F_{cur}>F_{BRP})$, calculated as percentages, of current fishing mortality, F_{cur}(0.120/year), exceeding F_{BRPs} after repeating the standard scenario 1000 times. Numbers in the parentheses provide the ranges of relative changes in means and SDs from random Monte Carlo simulation with data for female Japanese eel (*Anguilla japonica*) in the Kao-Ping River in southern Taiwan.

F_{BRP}	Mean	SD
F_{max}	0.156 (99.95–100.04%)	1.6×10^{-3} (97.23–103.89%)
$F_{0.1}$	0.111 (99.96–100.03%)	9.2×10^{-4} (97.24–103.90%)
$F_{30\%}$	0.129 (99.97–100.03%)	8.7×10^{-4} (97.32–104.44%)
$F_{50\%}$	0.073 (99.97–100.03%)	4.6×10^{-4} (97.31–104.43%)
$P(F_{cur}>F_{max})$	13.44	0.47
$P(F_{cur}>F_{0.1})$	56.44	0.70
$P(F_{cur}>F_{30\%})$	35.48	0.65
$P(F_{cur}>F_{50\%})$	94.31	0.32

$T^{S}_{F_{BRP}}$ = the same statistic of the same F_{BRP} from the standard scenario.

The sensitivity of an F_{BRP} also has to be distinguished from the random variation that results from Monte Carlo simulation, namely the variation that results from the incorporation of random errors in M, length-weight relationship, and maturation process. To understand the scale of this random variation, the standard scenario (scenario 1, without any biasesor imprecision in parameters) was repeated 1000 times, producing1000 corresponding RC values for the means and SDs of F_{BRPs}. The minimum and maximum values of RC from these 1000 repetitions of scenario 1 were used as the lower and upper limits of random variation from the Monte Carlo simulation. The effect of changes in the mean or SD of a parameter was considered significant only when its RC is lower than the minimum or larger than the maximum RC. All the computations and simulations were completed in R, vers. 3.1.0 (R Core Team, 2014).

Results

Magnitude of the random variation from Monte Carlo simulation

Running the Monte Carlo simulation of the standard scenario 1000 times produced RC values for the means of F_{max}, $F_{0.1}$, $F_{30\%}$,and $F_{50\%}$ that ranged from 99.95% to 100.04%, from 99.96% to 100.03, from 99.97% to 100.03, and from 99.99% to 100.03%, respectively (Table 3). The SD values of the F_{BRPs} had larger RC values that ranged from 97.23% to 103.89% for F_{max}, from 97.24% to 103.90% for $F_{0.1}$, from 97.32% to 104.44% for $F_{30\%}$, and from 97.31% to 104.43% for $F_{50\%}$(Table 3). Therefore, variation of RC within 0.05% for the mean and within 4.50% for the SD of the F_{BRP} was applied as the criterion for significance of effects; that is, we considered the effect of changing one parameter on the F_{BRP} to be significant when the resultant RC was wider than this criterion.

Sensitivity of reference points from the YPR model

The means of F_{BRPs} from the YPR model, namely F_{max} and $F_{0.1}$, were sensitive to both the means of M and K, which had similar trends but different magnitudes (Fig. 1, left panels). The RC values for the means of F_{max} and $F_{0.1}$ decreased slowly to 75–80% when M and K decreased to 5%. As M and K increased to 1000%, their RC values rose with an accelerating trend, especially for F_{max}, to more than 12,000% and 1100%, respectively. However, the means of F_{max} and $F_{0.1}$ were not sensitive to changes in L_∞ and ε_{GR} because their RC varied less than 0.05%. The ε_M had marginal effects on the mean of F_{max} and $F_{0.1}$, given that the RC was around 100.6% when ε_M became 1000% (Fig.1, left panels). The SD values of F_{max} and $F_{0.1}$ were also sensitive to the means of M and K with similar accelerating trends. The SD of F_{max} was more sensitive to changes in M and K than was the SD of $F_{0.1}$ (Fig. 1, right panels). In addition, the SD values of F_{max} and $F_{0.1}$ were nearly related linearly to ε_M. Similar to the means, the SD values of F_{max} and $F_{0.1}$ did not show significant sensitivity to L_∞ and ε_{GR}, and their RC values did not exceed the significance level of 4.50%.

Sensitivity of reference points from the SPR model

The means of F_{BRPs} from the SPR model, $F_{30\%}$, and $F_{50\%}$, were sensitive to the mean of M, but their RC values (from 90% to 170%; Fig. 2, left panels) were smaller than those of F_{max} and $F_{0.1}$. When K decreased to 40%, the RC for the mean of $F_{30\%}$ and $F_{50\%}$ reached a minimum of around 80%. As K increased to 1000%, the RC of the means of $F_{30\%}$ and $F_{50\%}$ increased to 300% and 400%. They also were affected by L_∞ such that the RC was around 85–125% as L_∞ increased from 50% to 200%. Neither ε_M nor ε_{GR} affected the means of $F_{30\%}$ and $F_{50\%}$. The SD values of $F_{30\%}$ and $F_{50\%}$ showed the highest sensitivity to the mean of M, with

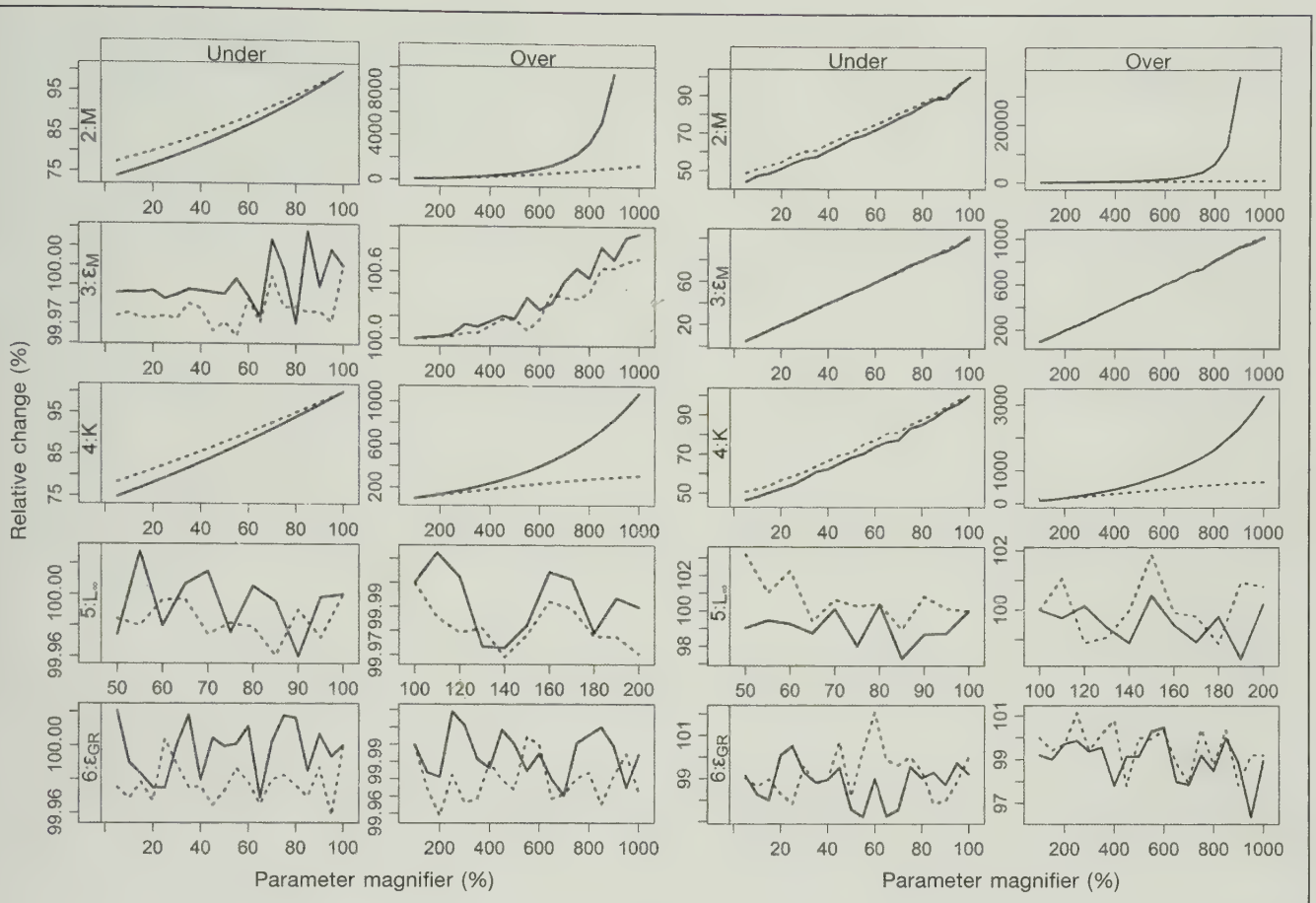

Figure 1

Relative changes determined from Monte Carlo simulation with data collected during 1998–2006 for female Japanese eel (*Anguilla japonica*) in the Kao-Ping River in southern Taiwan. The relative changes are measured as percentages for the means (shown in the left panels) and standard deviations (SD; shown in the right panels) of fishery-mortality–based reference points(F_{BRPs}) in scenarios 2–6 of the yield-per-recruit model, where the mean and SD of the natural mortality (M and ε_M), the von Bertalanffy growth coefficient (K), the asymptotic length (L_∞), and the multiplicative error in the growth curve (ε_{GR}) were under-specified from 5% to 95% and over-specified from 150% to 1000% (except forvalues of L_∞ that went from 50% to 200%). In each graph, the solid line indicates fishing mortality at which yield per recruit is at its maximum, and the dashed line indicates fishing mortality at which the increase of yield per recruit is only 10% of the increase of yield per recruit when fishing mortality is zero. Because of the large variation in RC values for the different scenarios, the scales of the y-axes differ greatly to allow changes to be seen. Under=underspecified parameters; Over=overspecified parameters; ε_M=the SD of M; F_{cur}=current fishing mortality and; ε_{Fcur}=SD of F_{cur}.

the RC changing from 70% to around 4000%. The parameter K had high influence on the SD values of $F_{30\%}$ and $F_{50\%}$, with RC changing from 20% to 1500% (Fig. 2, right panels). The parameters ε_M and L_∞ had considerable effects on the SD values of $F_{30\%}$ and $F_{50\%}$, with RC ranging from 90% to 400% and from 40% to 150%, respectively. The SDs of $F_{30\%}$ and $F_{50\%}$ were not affected by ε_{GR}.

Sensitivity of the composite risks of overfishing

The composite risks of growth overfishing (F_{cur} exceeding F_{max} and $F_{0.1}$) decreased with increasing means of M and K and did not depend on changes in L_∞, ε_{GR}, and ε_M (Fig. 3). The risks of recruitment overfishing (F_{cur} exceeding $F_{30\%}$ and $F_{50\%}$) showed the greatest sensitivity to K followed by M. The risk of recruitment overfishing was affected also by changes in L_∞ but with less sensitivity. The parameters ε_M and ε_{GR} did not contribute to noticeable changes in the risks of overfishing. The risks of both growth and recruitment overfishing showed strong sensitivity to both the mean and SD of F_{cur}. As the mean of F_{cur} increased from around 150% to 225%, the risks approached 100%. The risks of overfishing decreased with increasing SD for F_{cur}.

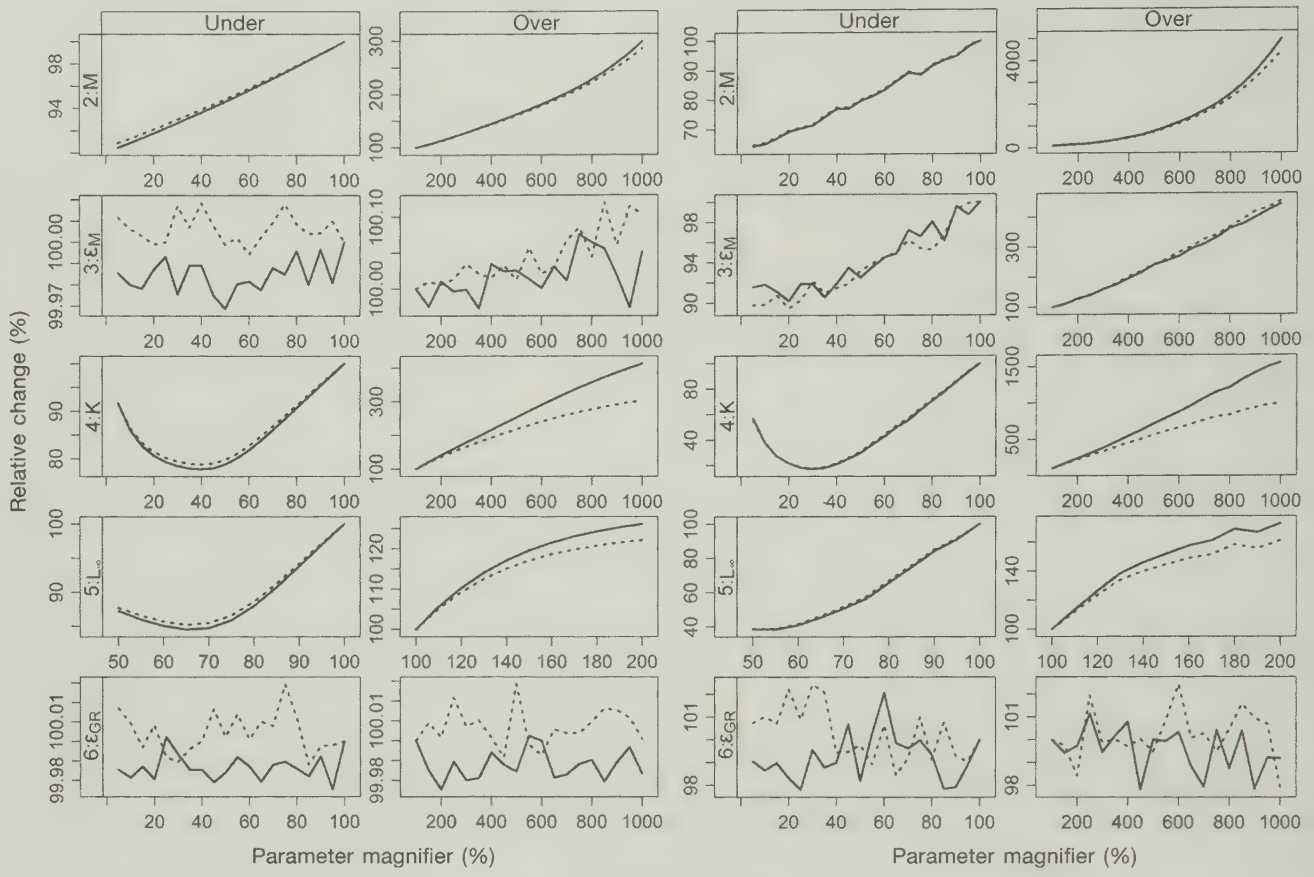

Figure 2

Relative changes from the Monte Carlo simulation with data collected during 1998–2006 for female Japanese eel (*Anguilla japonica*) in the Kao-Ping River in southern Taiwan. The relative changes are measured as percentages, for the means (shown in the left panels) and SDs (shown in the right panels) of fishery-mortality–based reference points(F_{BRPs}) in scenarios 2–6 of the spawning-biomass-per-recruit model, where the mean and SD of the natural mortality (M and ε_M), the von Bertalanffy growth coefficient (K), the asymptotic length (L_∞), and the multiplicative error in the growth curve ($_{GR}$) were under-specified from 5% to 95% and over-specified from 150% to 1000% (except forvalues of L_∞ that went from 50% to 200%). In each graph, the solid line indicates the fishing mortality rate at which the spawning biomass per recruit (SPR) is 30% of the SPR when fishing mortality is zero, and the dashed line indicates the fishing mortality rate at which the SPR is 50% of the SPR when fishing mortality is zero. Because of the large variation in RC values for the different scenarios, the scales of the y-axes differ greatly to allow changes to be seen. Under=underspecified parameters; Over=overspecified parameters.

Effects of multiplicative error in the length–weight relationship

The changes in ε_{LW} resulted in nonsignificant changes in the mean and SD of the 4 F_{BRPs}. They also did not affect the composite risks of exceeding these F_{BRPs}.

Discussion

Effects of uncertainty in mean and SD of natural mortality

Estimates of the mean of M are usually highly uncertain, possibly because of the lack of appropriate data for direct estimation, data such as those from tag–recapture experiments (Vetter, 1988). As M increases, the YPR curve becomes flatter with a decreasing maximum value and decreasing slope at the origin (fig. 17.18 in Beverton and Holt, 1957). This change in the shape of YPR curve accounts for the nonlinear accelerating trend of F_{max} and $F_{0.1}$ found in our study. Uncertainty in the mean (bias) of M can also cause significant biases in results of the model for SPR, particularly at a high level of fishing mortality (Goodyear, 1993). A higher mean of M led to a steeper SPR curve, but the general shape of the curve was not altered, explaining the lower sensitivity of $F_{30\%}$ and $F_{50\%}$ to M. On the other hand, the SD (imprecision) of M resulted

in significant changes only in the SDs of the 4 F_{BRPs} examined. Therefore, as indicated in the Appendix Figure, the risks of both growth and recruitment overfishing were affected more by the changes in the mean of Mthan by changes in the SD. The bias in M seems to be more important than the imprecision in M in influencing the risks of overfishing.

Effects of uncertainty in growth parameters

The shape of the YPR curve also was altered by K (fig. 17.22 in Beverton and Holt, 1957). The flattening of the YPR curve with decreasing K accounts for the accelerating increase in the mean and SD of F_{max}. On the other hand, Beverton and Holt (1957) found that the changes in W_∞(equivalent to L_∞ under the same length–weight relationship) did not affect the shape of the YPR curve. This insensitivity of the YPR shape on L_∞ explains our finding that changes in L_∞ did not affect the mean and SD of F_{max} and $F_{0.1}$ or the corresponding risk of growth overfishing.

The peaks in the values of RC in the means and SDs of $F_{30\%}$ and $F_{50\%}$ when K and L_∞were around 40–60% possibly resulted from the use of a length-dependent maturation curve for anguillids (Davey and Jellyman, 2003) in the calculation of SPR. In the cases with extremely small values of K or L_∞, the proportion of mature eels was close to zero even at the maximum age (16 years). A very small part of the spawning biomass was lost because of fishing, consequently resulting in higher $F_{30\%}$ and $F_{50\%}$ values.

Effects of current fishing mortality

The bias and imprecision in F_{cur} played an important role in determining risks of overfishing. Greater effects due to changes in the mean of F_{cur} on the risks of both growth and recruitment overfishing were expected because differences in the mean played an important part in influencing the composite risk, as in the example of 2 standard normal random variables (Appdx Fig.). Given the same difference in the means, a larger SD leads to lower composite risks (Appendix. Figure, panels B and D), accounting for the observed decreasing risks of overfishing with increasing ε_{Fcur}. Given that F_{cur} is from the gamma distribution, decreasing composite risks with increasing ε_{Fcur} also resulted in the convergence of 4 risks of overfishing. This finding indicates that a high ε_{Fcur} value may mask the distinction between target (usually $F_{0.1}$ or $F_{50\%}$) and threshold (F_{max} or $F_{30\%}$) F_{BRPs} because the risks of target and threshold F_{brp} are similar.

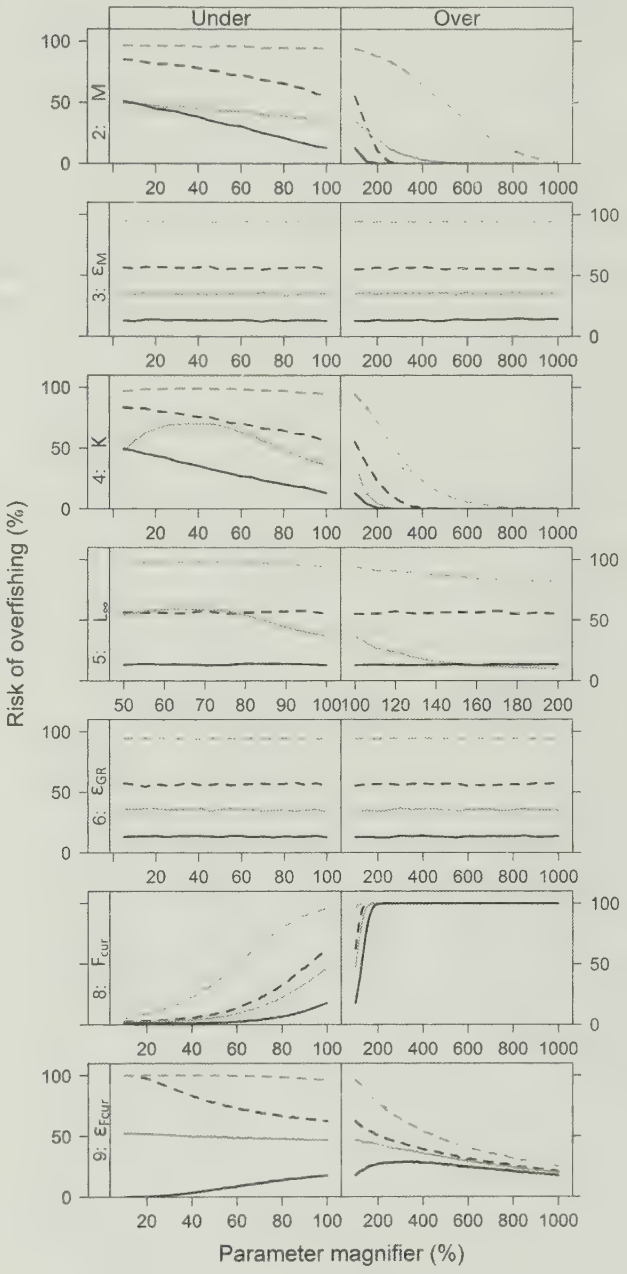

Figure 3

The composite risks of overfishing in scenarios 2–6, 8, and 9, where the mean and standard deviation (SD) of the natural mortality (M and ε_M), the von Bertalanffy growth coefficient (K), the asymptotic length (L_∞), the multiplicative error in the growth curve (ε_{GR}), and the mean and SD of current fishing mortality (F_{cur} and ε_{Fcur}) were under-specified from 5% to 95% and over-specified from 150% to 1000% (except forvalues of L_∞ that went from 50% to 200%). The black solid line indicates the composite risk of F_{cur} exceeding the fishing mortality at which yield per recruit is at its maximum, the black dashed line indicates the composite risk of F_{cur} exceeding the fishing mortality at which the increase of yield per recruit is only 10% of the increase of yield per recruit F=0,and the gray solid and dashed lines indicate the composite risk of F_{cur} exceeding the fishing mortality rates at which the spawning biomass per recruit (SPR) is 30% and 50% of the SPR when F=0.

The assumption of a gamma distribution of F_{cur} may be the reason for increasing risks of exceeding F_{max} when ε_{Fcur} lies between 5% and 200%. When ε_{Fcur} was 50% or less, the gamma distribution of F_{cur} resembled the normal distribution with density highly concentrated around its mean. Because F_{max} (0.151) was much larger than F_{cur} (0.120), the area of the distribution of F_{cur} that exceeded F_{max} became smaller and smaller as ε_{Fcur} decreased, resulting in lower risks.

Asymmetry in the sensitivities of reference points

The responses of the means and SDs of 4 F_{BRPs} to the changes in the means of M or K showed disproportionate increases, indicating that the means and SDs of F_{BRPs} were more sensitive to over-specification. This accelerating trend, arising from the nonlinear relationship between these parameters and F_{BRPs} (Schnute and Richards, 1998), indicates that under the same degree of misspecification (e.g., 50%) an over-specified mean of M or K could result in seriously overestimated values of F_{BRPs}. Consequently, the risks of overfishing would be underestimated, potentially leading to overexploitation.

In summary, bias in life history parameters, such as M, F_{cur}, K, and L_∞, resulted in considerable changes in the means and SDs of 4 selected F_{BRPs}: F_{max}, $F_{0.1}$, $F_{30\%}$, and $F_{50\%}$. Different degrees of the imprecision in the life history parameters did not affect the means of F_{BRPs} but substantially influenced their SDs. Over-specification of the mean of M and K led to larger values of RC in the means and SDs of F_{BRPs} than did under-specification of the means of M and K.

The composite risks of F_{cur} exceeding these 4 F_{BRPs} were affected mainly by bias in the life history parameters rather than by their imprecision. Both bias and imprecision in F_{cur} played crucial roles in determining the risks of F_{cur} exceeding these 4 F_{BRPs}. The variation in growth curves and length–weight relationships did not affect results of the per-recruit models. Our results agreed with those of previous studies without consideration of parameter uncertainty, indicating that they can apply to YPR and SPR models for other species. We recommend 1) minimizing the bias in the life history parameters, especially bias in M, K, and F_{cur}, and 2) maximizing the precision in F_{cur} as the most relevant approaches for development of correct estimates of F_{BRPs} and determining risks of overfishing.

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Literature cited

Beverton, R. J. H., and S. J. Holt.
1957. On the dynamics of exploited fish populations, 533 p. Great Britain Fish. Investig. Ser. II. Ministry of Agriculture, Fisheries and Food, Fisheries Laboratory, Lowestoft, U.K.

Chang, Y. J., C.-L. Sun, Y. Chen, S.-Z. Yeh, and W.-C. Chiang.
2009. Incorporating uncertainty into the estimation of biological reference points for a spiny lobster (*Panuliruspenicillatus*) fishery. N.Z.J. Mar. Freshw. Res. 43:429–442.

Charles, A. T.
1998. Living with uncertainty in fisheries: analytical methods, management priorities and the Canadian ground fishery experience. Fish. Res. 37:37–50.

Chen, Y., and C. Wilson.
2002. A simulation study to evaluate impacts of uncertainty on the assessment of American lobster fishery in the Gulf of Maine. Can. J. Fish. Aquat. Sci. 59:1394–1403.

Cope, J. M., and A. E. Punt.
2007. Admitting ageing error when fitting growth curves: an example using the von Bertalanffy growth function with random effects. Can. J. Fish. Aquat. Sci. 64:205–218.

Cubillos, L. A., R. Alarcón, and A. Brante.
1999. Empirical estimates of natural mortality for the Chilean hake (*Merlucciusgayi*): evaluation of precision. Fish. Res. 42:147–153.

Davey, A. J. H., and D. J. Jellyman.
2003. Sex determination in freshwater eels and management options for manipulation of sex. Rev. Fish Biol. Fish. 15:37–52.

Formacion, S. P., J. M. Rongo, and V. C. Sambilay Jr.
1991. Extreme value theory applied to the statistical distribution of the largest lengths of fish. Asian Fish. Sci. 4:123–135. [Available at website.]

Froese, R., and C. Binohlan.
2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. J. Fish Biol. 56:758–773.

Gabriel, W. L., and P. M. Mace.
1999. A review of biological reference points in the context of the precautionary approach. *In* Proceedings of the fifth national NMFS stock assessment workshop: providing scientific advice to implement the precautionary approach under the Magnuson-Stevens Fishery Conservation and Management Act; Key Largo, FL, 24–26 February 1998 (V. R. Restrepo, ed.), p. 34–45. NOAA Tech. Memo. NMFS–F/SPO–40.

Goodyear, C. P.
1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *In* Risk evaluation and biological reference points for fisheries management (S. J. Smith, J. J. Hunt, and D. Rivard, eds.), p. 67–81. Can. Spec. Publ. Fish. Aquat. Sci. 120.

Grabowski, R., and Y. Chen.
2004. Incorporating uncertainty into the estimation of the biological reference points $F_{0.1}$ and F_{max} for the Maine

green sea urchin (*Strongylocentrotus droebachiensis*) fishery. Fish. Res. 68:367–371.

Hall, H. G., S. A. Hesp, and I. C. Potter.
2004. A Bayesian approach for overcoming inconsistencies in mortality estimates using, as an example, data for *Acanthopagrus latus*. Can. J. Fish. Aquat. Sci. 61:1202–1211.

Han, Y.-S., and W.-N. Tzeng.
2006. Use of the sex ratio as a means of resource assessment for the Japanese eel *Anguilla japonica*: a case study in the Kaoping River, Taiwan. Zool. Stud. 45:255–263.

Helser, T. E., and H.-L. Lai.
2004. A Bayesian hierarchical meta-analysis of fish growth: with an example for North American largemouth bass, *Micropterus salmoides*. Ecol. Model. 178:339–416.

Hilborn, R., and C. J. Walters
1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty, 570 p. Chapman & Hall, London.

Jiao, Y., Y. Chen, and J. Wroblewski.
2005. An application of the composite risk assessment method in assessing fisheries stock status. Fish. Res. 72:173–183.

Keller, A. A., K. J. Molton, A.C. Hicks, M. Haltuch, and C. Wetzel.
2012. Variation in age and growth of greenstriped rockfish (*Sebastes elongatus*) along the U.S. west coast (Washington to California). Fish. Res. 119:80–88.

King, M.
2007. Fisheries biology, assessment and management, 2nd ed., 400 p. Wiley-Blackwell, Oxford, U.K.

Lai, H. L., and D. R. Gunderson.
1987. Effects of ageing errors on estimates of growth, mortality and yield per recruit for walleye pollock (*Theragra chalcogramma*). Fish. Res. 5:287–302.

Lin, Y.-J., S.-L. Chang, M.-Y. Chang, S.-H. Lin, T.-I. Chen, M.-S. Su, W.-C. Su, and W.-N. Tzeng.
2010b. Comparison of recapture rates and estimates of fishing and natural mortality rates of Japanese Eel *Anguilla japonica* between different origins and marking methods in a mark-recapture experiment in the Kaoping River, southern Taiwan. Zool. Stud. 49:616–624.

Lin, Y.-J., Y.-J. Chang, C.-L. Sun, and W. N. Tzeng.
2010a. Evaluation of the Japanese eel fishery in the lower reaches of the Kao-Ping River, southwestern Taiwan using a per-recruit analysis. Fish. Res. 106:329–336.

Lin, Y.-J., N.-J. Su, B. M. Jessop, W.-C. Chiang, and C.-L. Sun.
2012. Errors in coefficient or expected value? Effects of different methods on simulated values for a linear model and the nonlinear von Bertalanffy growth model. J. Fish. Soc. Taiwan 39:23–34.

Lin, Y.-J., and C.-L. Sun.
2013. Estimation of natural mortality of Japanese eel (*Anguilla japonica*) using multiple indirect methods. J. Fish. Soc. Taiwan 40:171–182.

Lin, Y.-J., and W.-N. Tzeng.
2008. Effects of shrimp net and cultured eels on the wild population of Japanese eel *Anguilla japonica* in the Kao-Ping River, Taiwan. J. Fish. Soc. Taiwan 35:65–73.
2009. Modelling the growth of Japanese eel *Anguilla japonica* in the lower reach of the Kao-Ping River, southern Taiwan: an information theory approach. J. Fish Biol. 75:100–112.
2010. Vital population statistics based on length frequency analysis of the exploited Japanese eel (*Anguilla japonica*) stock in the Kao-Ping River, southern Taiwan. J. Appl. Ichthyol. 26:424–431.

Mace, P. M.
1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Can. J. Fish. Aquat. Sci. 51:110–122.

Pascual, M. A., and O. O. Iribarne.
1993. How good are empirical predictions of natural mortality? Fish. Res. 16:17–24.

Peterman, R. M.
2004. Possible solutions to some challenges facing fisheries scientists and manager. ICES J. Mar. Sci. 61:1331–1343.

Prager, M. H., C. E. Porch, K. W. Shertzer, and J. F. Caddy.
2003. Target and limits for management of fisheries: a simple probability-based approach. N. Am. J. Fish. Manage. 23:349–361.

Quinn, J. T., II, and R. B. Deriso.
1999. Quantitative fish dynamics, 560 p. Oxford Univ. Press, New York.

R Core Team.
2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available at website, accessed May 2014.]

Restrepo, V. R., and W. W. Fox Jr.
1988. Parameter uncertainty and simple yield-per-recruit analysis. Trans. Am. Fish. Soc. 117:282–289.

Seber, G. A. F.
1982. The estimation of animal abundance and related parameters, 2nd ed., 672 p. Charles Griffin & Co., London.

Schnute, J. T., and L. J. Richards.
1998. Analytical models for fishery reference points. Can. J. Fish. Aquat. Sci. 55:515–528.

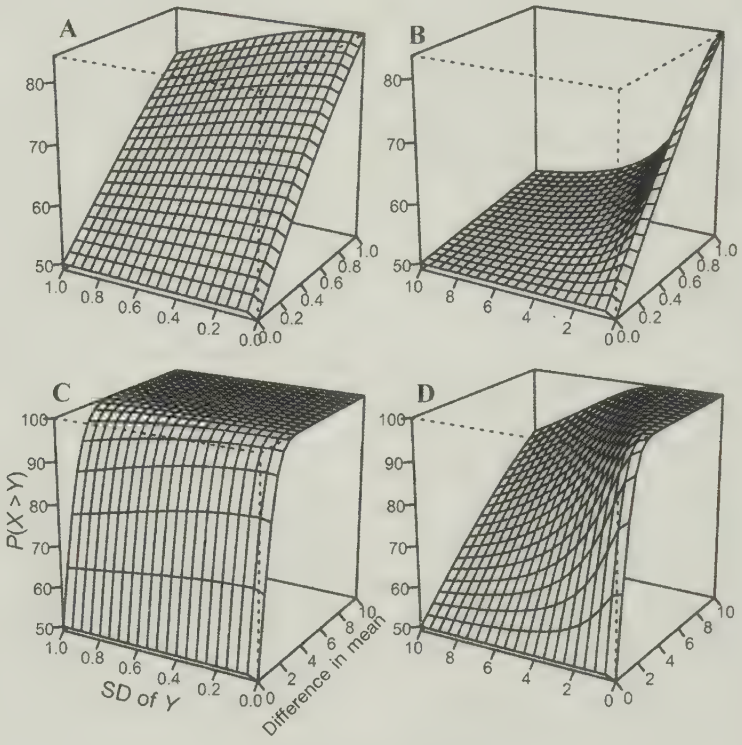
Sissenwine, M. P., and J. G. Shepherd.
1987. An alternative perspective on recruitment overfishing and biological reference points. Can. J. Fish. Aquat. Sci. 44: 913–918.

United Nations.
1995. Agreement for the implementation of the provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 relating to the conservation and management of straddling fish stock and highly migratory fish stocks. United Nations Conference on Straddling Fish Stocks and Highly Migratory Fish Stocks, Sixth session, New York, 24 July–4 August 1995. A/CONF. 164/37, 40 p. [Available at website.]

Vetter, E. F.
1988. Estimation of natural mortality in fish stocks: a review. Fish. Bull. 86:25–43.

Appendix

This appendix presents changes in composite risks of 2 random variables, X and Y, under different means and standard deviations.



Appendix Figure

The composite risks of Y exceeding X, or P(Y>X), measured in percentages, in which X is a standard normal variable (X~N[0,1]) and Y is a random normal variable with changing mean and standard deviation (SD) (μ_Y, σ_Y). (**A**) Reference case: (μ_Y, σ_Y)=(from 0 to 1, from 0.05 to 1); (**B**) large SD of Y case: (μ_Y, σ_Y)=(from 0 to 1, from 0.5 to 10); (**C**) large difference in mean case: (μ_Y, σ_Y)=(from 0 to 10, from 0.05 to 1); and (**D**) large difference in mean and SD of Y case: (μ_Y, σ_Y)=(from 0 to 10, from 0.5 to 10).

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Seasonal migrations of morphometrically mature male snow crab (*Chionoecetes opilio*) in the eastern Bering Sea in relation to mating dynamics

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Abstract—Seasonal migration of commercial-size (≥102 mm carapace width [CW]), morphometrically mature (MM) snow crabs (*Chionoecetes opilio*) from the eastern Bering Sea was examined in relation to the summer distribution of mature females to identify spatiotemporal overlap of males and females and determine the likelihood of mating associations for specific reproductive stages. Depth variation associated with this migration was examined to determine whether seasonal migrations contribute to previously recognized spatial differences in distributions of commercial-size males caught in the winter fishery and in the National Marine Fisheries Service summer bottom trawl survey. Depth data from 33 data storage tags attached to commercial-size MM males during 2010 and 2011 indicated that most males moved inshore during spring—a movement that would allow them to mate with multiparous females but not with pubescent-primiparous females. Smaller tagged males (100–102 mm CW) underwent more extensive inshore migrations, and several of them traveled more than 100 km in one direction. Both tagging and distribution data indicated that most commercial-size MM males remained predominantly on the outer shelf throughout the year (despite some inshore movements during spring) and, therefore, these males did not contribute greatly to the spatial differences observed between winter and summer.

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Migrations of snow crabs (*Chionoecetes opilio*) differ between sexes and among different size classes, resulting in distributions that are highly structured and complex (Ernst et al., 2005). In the eastern Bering Sea, these migrations depend partially on bottom temperature gradients (Ernst et al., 2005) and can vary annually depending on the extent of the "cold pool" (Kotwicki and Lauth, 2013), a near bottom layer of cold (<2°C) water that forms across mid-depths (50–100 m) of the eastern Bering Sea shelf. On the basis of data from the eastern Bering Sea shelf collected during the National Marine Fisheries Service (NMFS) annual summer bottom-trawl survey, immature crabs of both sexes undertake down-slope ontogenetic migrations that are generally from the northeast to the southwest (Otto, 1998; Zheng et al., 2001; Ernst et al., 2005). Upon reaching full maturity, both sexes undergo a terminal molt in the spring, after which they are thought to continue to migrate into deeper water (Oresanz et al., 2004; Ernst et al., 2005; Parada et al., 2010). For commercial-size males, ≥102 mm in carapace width (CW), this migration is assumed to culminate on the outer shelf (depths of 100–200 m), where the winter commercial fishery is concentrated (Orensanz et al., 2004). Less is known about smaller terminally molted males, but they are assumed to reside inshore of the commercial-size males.

Male migrations likely differ before and after the terminal molt. Because the transformation from a small-clawed "adolescent" stage to a large-clawed morphometrically mature (MM) stage coincides with the terminal molt for males, these stages have been distinguished by using the relationship of carapace width (CW) to chela height (CH) (Comeau and Conan, 1992; Stevens et al., 1993; Rugolo et al.[1]; Tamone et al., 2007). Because members of a cohort can reach maturity over multiple ages, the size distribution of MM males overlaps that of adolescent males. Although adolescent males are sometimes capable of mating, MM males

[1] Rugolo, L., D. Pengilly, R. MacIntosh, and K. Gravel. 2005. Reproductive potential and life history of snow crabs in the eastern Bering Sea. *In* Bering Sea snow crab fishery restoration research: final comprehensive performance report. (D. Pengilly and S. E. Wright, eds.), p. 57–323. NOAA Cooperative Agreement NA17FW1274. Div. Commer. Fish., Alaska Dep. Fish Game, Juneau, AK.

have a distinct competitive advantage in securing mates (Sainte-Marie et al., 1997).

Seasonal inshore migrations of post-terminal-molt MM male snow crabs, at least in waters of eastern Canada, have been attributed to mating behavior. These migrations are either targeted toward pubescent-primiparous females, those that will soon terminally molt and then brood their first clutch after mating, or toward multiparous females, those carrying clutches in subsequent years (Lovrich et al., 1995; Sainte-Marie et al., 2008). In the eastern Bering Sea, pubescent-primiparous females reside in shallower water and mate 1–3 months (February to March) earlier than multiparous females (Somerton, 1982; Ernst et al., 2005; Kruse et al., 2007). Peak spawning and subsequent mating among multiparous females in the eastern Bering Sea occur between March and April (Rugolo[2]), although a small percentage may be in a receptive condition until July (Somerton, 1981).

Whether commercial-size MM males in the eastern Bering Sea undergo a seasonal inshore migration for the purpose of mating is unknown. If multiparous females in the eastern Bering Sea are relatively sedentary, as they are in eastern Canada (Lovrich et al., 1995), an inshore migration by commercial-size MM males may be necessary for successful mating. Earlier and more extensive inshore migrations would certainly be required to mate with pubescent-primiparous females (Parada et al., 2010). Theoretically, there may not be a need to migrate toward and mate with multiparous females because these females can store sperm over multiple years (Sainte-Marie and Carrière, 1995). However, depending on the sex ratios of functionally mature crabs, ratios that can affect mate choice (Sainte Marie et al., 2008; e.g., the southern Tanner crab [*C. bairdi*], Webb and Bednarski, 2010), most multiparous females are presumed to mate annually if males are available. An exception to this assumption occurs among some females that reside in colder-water areas (<1.5°C) of the eastern Bering Sea and that spawn biennially (Rugolo et al.[1]).

Compared with the ontogenetic migrations of juvenile snow crabs in the eastern Bering Sea, little is known about the seasonal migration patterns of MM males because of the paucity of sampling during times other than those of the NMFS summer bottom trawl survey and the winter commercial fishery. The offshore migration of recently terminally molted MM males in the eastern Bering Sea was demonstrated by a study of the Alaska Department of Fish and Game (ADFG), during which MM males were tagged with spaghetti tags during summer, on the middle shelf, and many were recaptured near the outer shelf during the following winter snow crab fishery (Gravel et al., 2006; Pengilly[3]). However, because the fishery and, therefore, recaptures occur only on the outer shelf, the fraction of MM males that migrate to the outer shelf is unknown, and nothing is known about the possibility of these males migrating back to the middle shelf. Furthermore, because of the reliance on the fishery for recaptures, ADFG tagged only commercial-size males, and information on migration and distribution for small MM males (70–100 mm CW), which are prevalent in the eastern Bering Sea (Otto, 1998) and potentially important contributors to breeding, is lacking.

For commercial-size MM males, fishery managers have recognized a seasonal change in distribution, which is centered on the middle shelf of the eastern Bering Sea (bottom depth: <100 m) during the summer (Foy and Armistead, 2013) but shifts to the outer shelf (bottom depth: 100–200 m) from January to March when and where the fishery typically occurs (Orensanz et al., 2004; Bowers et al., 2011; Turnock and Rugolo[4]). Part of this distributional shift may be explained by the post-terminal-molt migration from the middle to the outer shelf (Orensanz et al., 2004), but an inshore spring migration by outer shelf males may contribute to this shift as well. Such a migration was documented by Lovrich et al. (1995), who found that MM male snow crabs <70 mm CW in the Gulf of St. Lawrence migrated to shallow water during early spring to mate with pubescent-primiparous females. In that study, however, large MM males tended not to migrate as far inshore or as early in the year as males <70 mm CW, therefore, limiting their mating to multiparous females.

Determining where and when large (>100 mm CW) and small (70–100 mm CW) MM males may migrate, and where they are spatially distributed in relation to pubescent-primiparous and multiparous females, can help elucidate which mating associations occur in the eastern Bering Sea. Although at least some large, recently terminally molted MM males migrate into deeper water after summer, it is not known whether these males seasonally migrate back inshore to mate with multiparous females or perhaps to shallower waters where pubescent-primiparous females reside (Parada et al., 2010). If seasonal inshore migrations do occur, it is not known how much they contribute to temporal differences in the spatial distribution of large MM males. For small MM males in the eastern Bering Sea, it is unclear what component of the mature female stock they associate with and mate with, because of the difficulty in recapturing small, tagged animals in the fishery and because the spatial distribution of these small MM males has not been examined separately from that of adolescents.

Using data storage tags (DSTs) that were capable of timed depth recordings and were deployed on com-

[2] Rugolo, L. 2014. Personal commun. Alaska Fish. Sci. Cent., Seattle, WA 98115.

[3] Pengilly, D. 2014. Personal commun. Alaska Dep. Fish Game, Kodiak, AK 99615.

[4] Turnock, B. J. and L. J. Rugolo. 2011. Stock assessment of eastern Bering Sea snow crab. In Stock assessment and fishery evaluation report for the king and Tanner crab fisheries of the Bering Sea and Aleutian Islands regions. 2011 crab SAFE, 37–168 p. North Pacific Fishery Management Council, Anchorage, AK [Available at website.]

mercial-size MM male snow crab, we examined the seasonal inshore and offshore migrations of these males to determine if their migrations contribute to the reported differences between distribution of MM male snow crab during summer and their distribution during winter. Second, by examining the summer distribution of mature females, we attempted to infer the components of the female stock that are associated with and mate with large MM males. Finally, we compared the distribution of both large and small MM males with that of mature females to assess the potential for size-specific male–female mating associations.

Materials and methods

Tagging

A total of 277 morphometrically mature male snow crab (96–134 mm CW) were tagged and released with pressure-and-temperature-recording DSTs on 18–22 April 2010 (n=120) and 7–8 March 2011 (n=157), near the end of each fishing season to ensure that tagged crab were not recaptured until the following year. Tagging operations occurred on the winter snow crab fishing grounds northwest of the Pribilof Islands at approximately 57°35 N in 2010 and about 100 km farther north at 58°30 N in 2011 (Fig. 1). DSTs were attached to spaghetti tags that were wrapped around the carapace of the crab between the first and second walking legs. Because male snow crab do not molt after they reach maturity, the effect of tagging on their behavior and mortality was assumed to be negligible. In April 2010, an additional 221 snow crab were tagged and released with numbered spaghetti tags without an attached DST as a control to determine whether the additional DST attachment affected capture rate, as well as to help examine site fidelity.

Crabs were captured and tagged aboard commercial crab pot fishing vessels *Kiska Sea* (in 2010) and *Pacific Sun* (in 2011) during normal commercial fishing operations, and they were released within 10 min of capture at the same location. All tagged male crabs had large claws and had new to slightly worn hard shells, conditions that predominated in the catches during the time of tagging. Only crabs that possessed all their limbs were selected for tagging. Tagged crabs were recaptured by commercial crab pot vessels during the following winter and spring snow crab fisheries in 2011 and 2012, and a tag reward program was implemented to provide an incentive to return tags. Locations where crabs were recaptured were documented by the fishermen who returned tags.

The DSTs, Cefas G5 Long Life[5] tags with 2 MB of memory (Cefas Technology Limited, Lowestoft, UK), measured depth (pressure) at 1-min intervals, with an accuracy of ±2 m and precision of <0.08 m, and temperature at 30-min intervals, with an accuracy of ±0.1°C and precision of 0.03°C. DSTs were bullet-shaped with dimensions of 8×31 mm and weighed 1 g in water.

Analyses of snow crab depth and ambient temperature

The shelf of the eastern Bering Sea slopes down gradually from northeast to southwest from the Alaska mainland (i.e., north of 58°N) out to the shelf break (bottom depth: approximately 200 m); therefore, changes in tag depth were used as proxies or indicators of inshore and offshore movements (Fig. 1). Because migrations likely included movements parallel to bottom depth contours (i.e., movements in northwest and southeast directions), exact migration pathways could not be determined.

For each recaptured crab, the recorded tag depths were plotted against time (e.g., month) to determine whether seasonal inshore and offshore migrations were made and whether migrations were consistent among all individuals. Temperatures also were plotted against time to document the temperatures of areas inhabited by snow crabs in the eastern Bering Sea. In a few cases, tag temperatures were compared with temperatures collected during the NMFS summer bottom trawl survey, to corroborate the position of a crab from release and recapture positions and to indicate their proximity to the cold pool.

Distribution of mature females

The distributions of primiparous and multiparous females were plotted with data from the 2010 and 2011 NMFS summer bottom trawl surveys (Foy and Armistead, 2013; Lauth and Nichol, 2013) to examine the extent to which their distributions overlapped with tagged MM males and to infer whether the migration of large MM males would be necessary to create mating opportunities. A critical assumption for this comparison was that the mature (i.e., primiparous and multiparous) female distributions observed during the summer survey were representative of the mature female distributions during the preceding winter–spring mating period. Primiparous females were identified as those females with uneyed eggs, clutch sizes 1/8 to 3/4 full, and soft to clean hard shell conditions. Multiparous females were identified as those females with either uneyed or eyed eggs, full clutch sizes, and hard shells with scratches or wear.

Distribution of morphometrically mature males

Broad-scale geographic distributions of MM male snow crabs during summertime were analyzed with data collected annually (1989–2011) during the NMFS summer bottom trawl survey (Foy and Armistead, 2013; Lauth and Nichol, 2013), where stations were fixed and positioned 37 km apart from each other. Distributions were plotted for 4 male categories; that is, for 2 different size classes (70–100 mm CW and >100 mm CW), each

[5] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

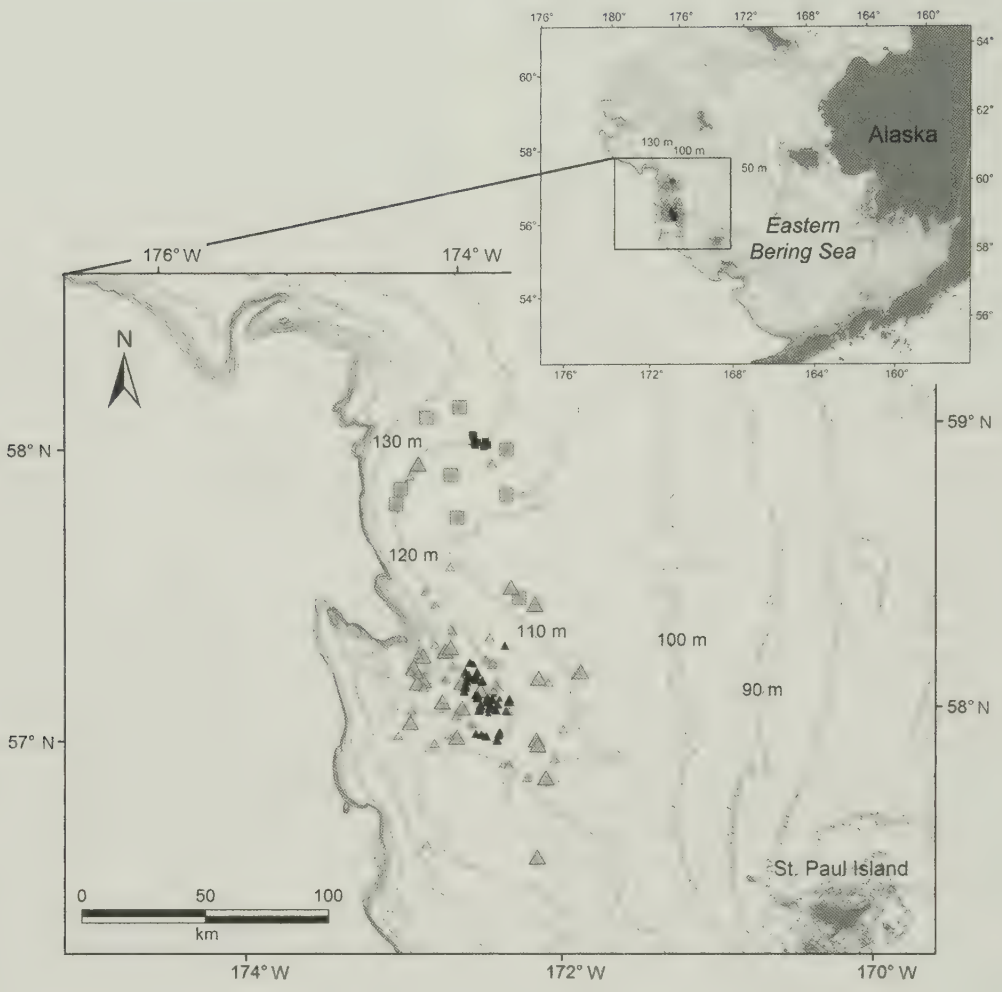

Figure 1

Release and recapture locations of morphometrically mature male snow crabs (*Chionoecetes opilio*) tagged with data storage tags (DSTs) during 2010 and 2011 in the eastern Bering Sea, northwest of the Pribilof Islands, which include St. Paul Island. Small black triangles indicate releases in 2010 of crabs with DSTs and spaghetti-only tags. Large and small gray triangles indicate recaptures of DSTs and spaghetti tags, respectively, from crabs released in 2010. Small black squares indicate releases in 2011 of crabs with DSTs. Large gray squares indicate recaptures of DSTs from crabs released in 2011. Lines with numbers indicate contours of bottom depths.

with 2 post-terminal-molt age categories representing MM males that recently terminally molted (in the current year; having a new shell) or in previous years (having an older shell). The new- and older-shell categories correspond to the shell conditions ≤2 and ≥3, respectively, as defined in Foy and Armistead (2013). MM males were distinguished from adolescent males by using a linear regression function relating ln(CH) to ln(CW) as calculated in Rugolo et al.[1], where for each measured specimen s, MM status was assigned where

$$CH_s > e^{1.2899 \times \ln(CW_s) - 2.8628}. \quad (1)$$

Because crabs measured for CH were subsampled from the catch at each station, their numbers were extrapolated to the entire catch at each station. Also, because males subsampled for CH were too few in number (mean: 24/station/year) to examine geographic distributions on an annual basis, data were pooled across years (1989–2011) for each station in the survey. For each survey station i, the relative proportion of MM males (*PROP*) was calculated with the following equation:

$$PROP_i = \frac{\Sigma_j N_{ij}}{\Sigma_{ij} N_{ij}}, \quad (2)$$

where N_{ij} = the extrapolated number of MM males at station i during year j.

If CHs were not measured within a particular year and station, each missing value of N_{ij} was estimated as the

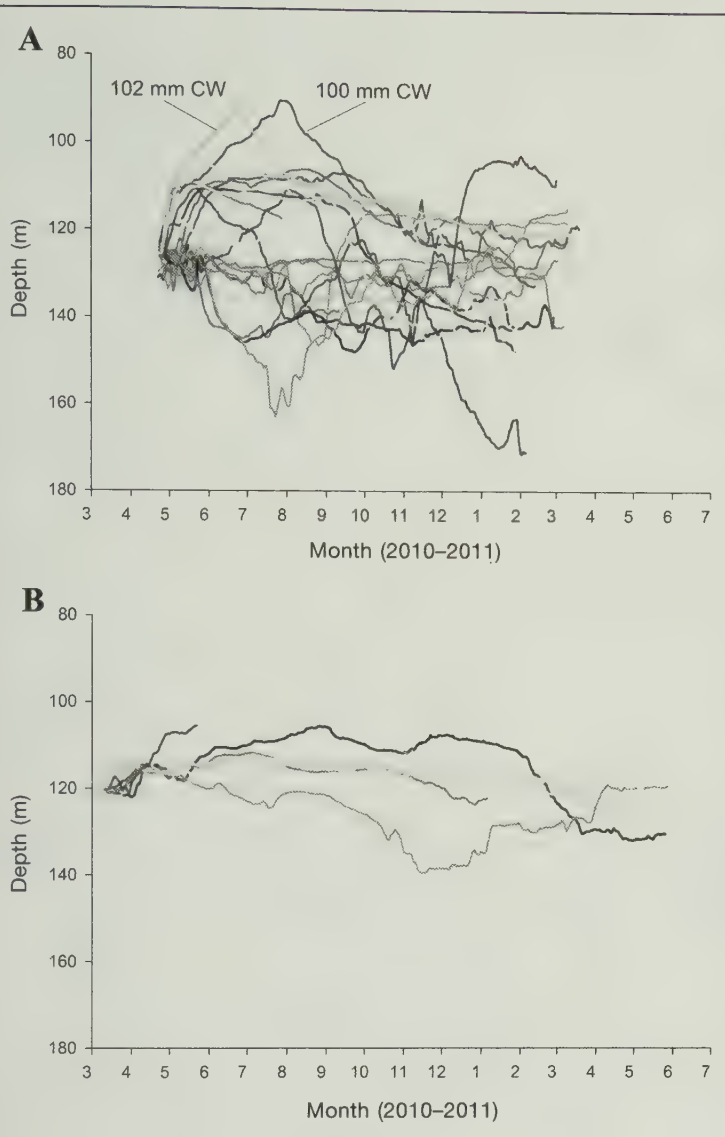

Figure 2

Timed depth recordings from data storage tags attached to morphometrically mature male snow crabs (*Chionoecetes opilio*) released in the eastern Bering Sea during (**A**) 2010 and (**B**) 2011. Two of the smallest tagged males (100 and 102 mm in carapace width) are indicated in panel A. See: http://dx.doi.org/10.7755/FB.113.3.7.

mean N_i during years when sampling occurred. Algebraically, this mean is expressed as

$$N_i = \frac{\Sigma_{ij} N_i}{n_i}, \quad (3)$$

where n_i = the number of years in which CHs were measured at station i.

Distribution of adolescent males

Adolescent males were also identified as above with the CH–CW regression provided in the previous section. Distributions were plotted as described previously for the size classes of 70–100 mm CW and >100 mm CW by using the data pooled across 1989–2011 and by using calculated relative proportions at each station.

Results

Time at liberty and recapture locations

A total of 33 male snow crabs with DSTs were recaptured, of which 4 individuals were 100–102 mm CW and the rest ranged in size from 106 to 126 mm CW. In addition, 43 males with only spaghetti tags (not DSTs) were recaptured with sizes ranging from 101 to 130 mm CW (Fig. 1).

Among males tagged with DSTs in 2010, 22 were recaptured in 2011 after 280–333 days at liberty and 1 was recaptured in 2012 after 640 days at liberty. Of the males released in 2011 with DSTs, 9 were recaptured in 2012 after 439–458 days at liberty. Among males tagged with spaghetti tags in 2010, 42 were at liberty between 274 and 319 days before recapture, and 1 other male was recaptured after 777 days. Recapture rates for snow crabs released in 2010 (and recaptured in 2011) were 18.3% (n=22) for those tagged with DSTs and 19.0% (n=42) for those tagged only with spaghetti tags, indicating essentially no difference in recapture rates between the 2 tag types. The attachment of the DSTs to spaghetti tags, therefore, was assumed to have no added effect on crab behavior or survival. Compared with males tagged in 2010, those males tagged in 2011 were recaptured later in the year (May–June, in 2012) and at a lower rate (5.7%; n=9), owing to ice conditions that limited access to the fishing area during winter and caused the fishing season to be extended (Gutierrez, 2012). Recapture locations of both types of tags indicate some site fidelity, as indicated by the low degree of area overlap between crabs recaptured in 2011 and 2012 and released approximately 100 km apart (Fig. 1).

Occurrence and extent of inshore–offshore migrations

Individual depth trajectories among tagged males were highly variable within the depth range they inhabited (90–172 m), indicating a wide variety of individual migration routes (Fig. 2, A and B). For the crabs released in 2010, 3 general movement patterns were observed: 1) extensive upslope (i.e., inshore) movements, or changes in depth, >20 m to depths <120 m within 1 month after tagging; 2) very limited upslope or

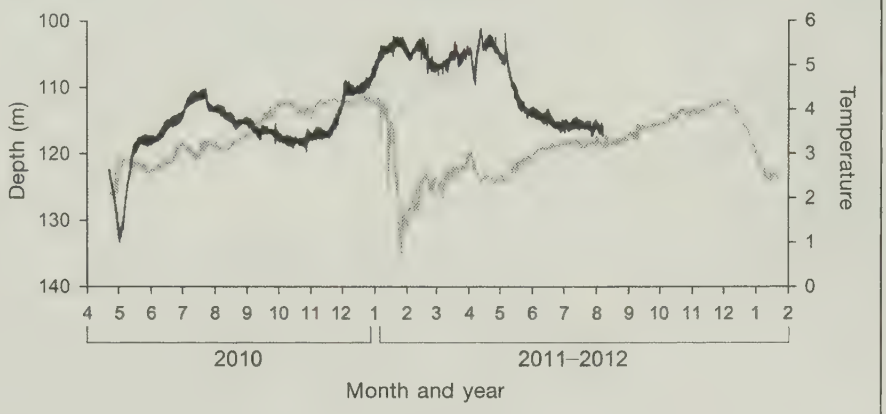

Figure 3

Timed depth (black line) and temperature (gray line) recordings from a data storage tag attached to a 100-mm (carapace width) morphometrically mature male snow crab (*Chionoecetes opilio*) released in the eastern Bering Sea in 2010. This crab was at liberty for 640 days, although the depth sensor ceased to function approximately 5 months before its recapture.

downslope movements (depth changes <10 m), remaining in depths >120 m; and 3) initial downslope movements of more than 20 m followed by extensive upslope movements, remaining in depths >120 m (Fig. 2A). For crabs released in 2011 (north of 2010 releases), all 9 of the males that were recovered moved upslope immediately after release in the spring, but their depth changes were less extensive than those of tagged males released in 2010 (Fig. 2B), with changes ranging from 7 to 16 m (mean: 10.5 m). Of the 5 males that were still at liberty during the following spring, in 2012, only 1 appeared to move upslope during the second spring.

Two of the 4 small tagged males (100–102 mm CW) undertook relatively long inshore migrations of ~100 km, in depths ranging from 120 to 90 m (Fig. 1) during the spring and summer followed by an offshore migration during fall and winter. They did not migrate together because the timing of their inshore and offshore movements was offset by about 1 month (Fig. 2A). A third small individual (100 mm CW), released in 2010 and at liberty 640 days, undertook inshore and offshore migrations in both 2010 and 2011, but it did so during different months and to differing extents (Fig. 3). During successive spring periods, it resided at different depths (by approximately 20 m) and different locations (separated by a distance of approximately 50 km), indicating that individuals can undergo variable migrations from year to year. The fourth small male (100 mm CW), released in 2011, migrated inshore but not to the extent of the other 3 small tagged male snow crabs.

Temperatures encountered

Temperatures encountered by the tagged males ranged from −0.5°C to 4.5°C (Fig. 4, A and B), although those males that were released at the more northern location in 2011 (n=9) experienced temperatures about 1°C colder (mean: 2.3°C) than the temperatures experienced by males (n=24) released farther south in 2010 (mean: 3.3°C). Seasonally, tagged males encountered the warmest temperatures during winter (~November–January) and the coldest temperatures during spring (~February–June). Annual differences in ambient temperature were apparent from DST data obtained from 2011 released males that were at liberty for more than 14 months (Fig. 4B); spring temperatures averaged 2.3°C in 2011 compared with 1.3°C in 2012. The coldest temperatures (<1°C) were encountered by the 2 males that, in 2010, migrated farthest inshore to a depth of 90 m (Fig. 4A), where, on the basis of the spatial distribution of bottom temperatures of the eastern Bering Sea shelf measured during the summer bottom trawl survey (Lauth, 2011), each of them migrated to the edge of the cold pool before initiating a return offshore migration. Both crabs remained at these colder temperatures for approximately 1 month before migrating offshore.

Proximity of mature females to tagged males

On the basis of the 2010, 2011, and 2012 data of the summer distributions of mature females, multiparous females were in close proximity (<10 km) to the locations where tagged males were released (Fig. 5, B, D, and F). In addition, the inshore migrations of tagged males during spring (Fig. 2) indicated that there was a broad overlap with multiparous females at the time of multiparous mating (March–April). The increase in the abundance of multiparous females in the vicinity of the tag release areas from 2010 to 2011 indicates that more females were available to tagged males for breeding in 2011 than in 2010. In contrast, primiparous females were found much farther east (by distances >50 km) of the tagged males during all 3 years (Fig. 5, A, C, and E).

Bathymetric overlap of tagged males and mature females

The extent of cross-shelf inshore migrations by tagged males, defined here as the minimum depth reached during their time at liberty, increased (e.g., decreasing minimum depth) with decreasing crab size (Fig. 6; linear regression: n=33, coefficient of determination [r^2]=0.39, P<0.001). Considering the depths where multiparous females were found during the NMFS summer bottom trawl surveys (Fig. 5), all tagged males occupied ar-

eas where these females resided, including 9 of the large males (>113 mm CW) that remained at depths >120 m and did not make a dedicated inshore migration. Therefore, they all had an opportunity to mate with multiparous females. In contrast, opportunities to mate with pubescent-primiparous females were unlikely given that these females were concentrated (Fig. 5) much farther to the east (shallower waters) and to the north. The two small tagged males that migrated to a 90-m depth were the exception; however, the months during which these males resided at a depth of 90 m (June–July), were well past the period of pubescent-primiparous mating (February–March).

Summer distributions of morphometrically mature and adolescent males

Small MM males (70–100 mm CW) were concentrated farther north and east (shallower water) of areas where large MM males (>100 mm CW) of the same shell condition resided, and new-shell MM males were concentrated farther east (shallower) than that where older-shell MM males of the same size class resided (Fig. 7, A–D). Large older-shell MM males were primarily distributed over the outer shelf (depths of 100–200 m), whereas new-shell MM males, from both size classes, were primarily distributed over the middle shelf (depths of 50–100 m), at least south of 59°N. Adolescent males of both size classes were distributed over the middle shelf (i.e., south of 59°N), and small individuals were distributed more to the northeast of areas where large individuals were distributed (Fig. 7, E and F).

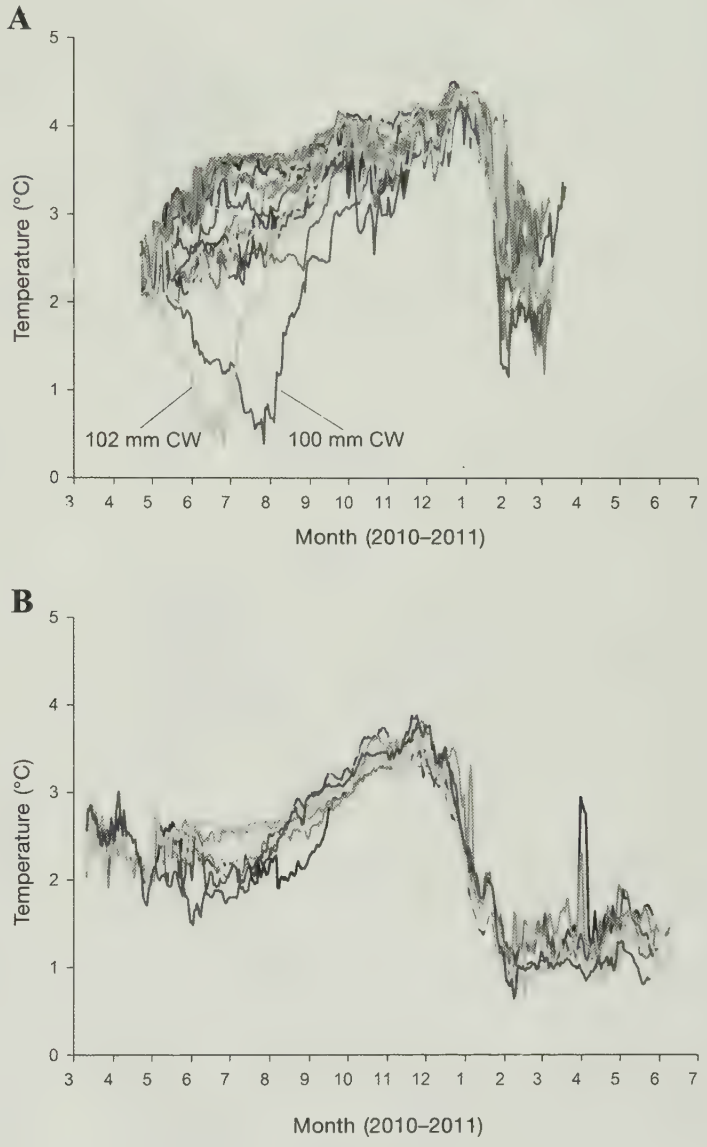

Figure 4

Mean daily temperature recordings from data storage tags attached to morphometrically mature male snow crabs (*Chionoecetes opilio*) released in the eastern Bering Sea during (**A**) 2010 and (**B**) 2011. Two of the smallest tagged males (100 and 102 mm in carapace width) are indicated in panel A. See: http://dx.doi.org/10.7755/FB.113.3.7.

Discussion

Most of the tagged MM males migrated inshore either shortly after their release during spring or during the following winter or spring. These migrations were not extensive enough to have contributed to the spatial difference in distributions between large males observed on the middle shelf during the NMFS summer bottom trawl survey and those males targeted on the outer shelf during the winter fishery. A seasonal shift in distribution of large males would be expected because of the fall migration of recently terminally molted males to deeper water, but this shift should be more prominent if these and older-shell MM males migrate back inshore every spring. Although springtime inshore migrations did occur, all but 2 of the tagged males remained on the outer shelf (depths >100 m) throughout their time at liberty.

The summer distribution of large, older-shell MM males (Fig. 7D) in waters deeper than 100 m confirmed the supposition that few of these individuals migrated back inshore to the middle shelf. The highest concentrations of large males found over the middle shelf (depths 50–100 m) during the summer survey (Orensanz et al., 2004; Turnock and Rugolo[4]), therefore, likely were not composed of MM males that seasonally migrated inshore but of recently terminally molted MM males that had yet to migrate

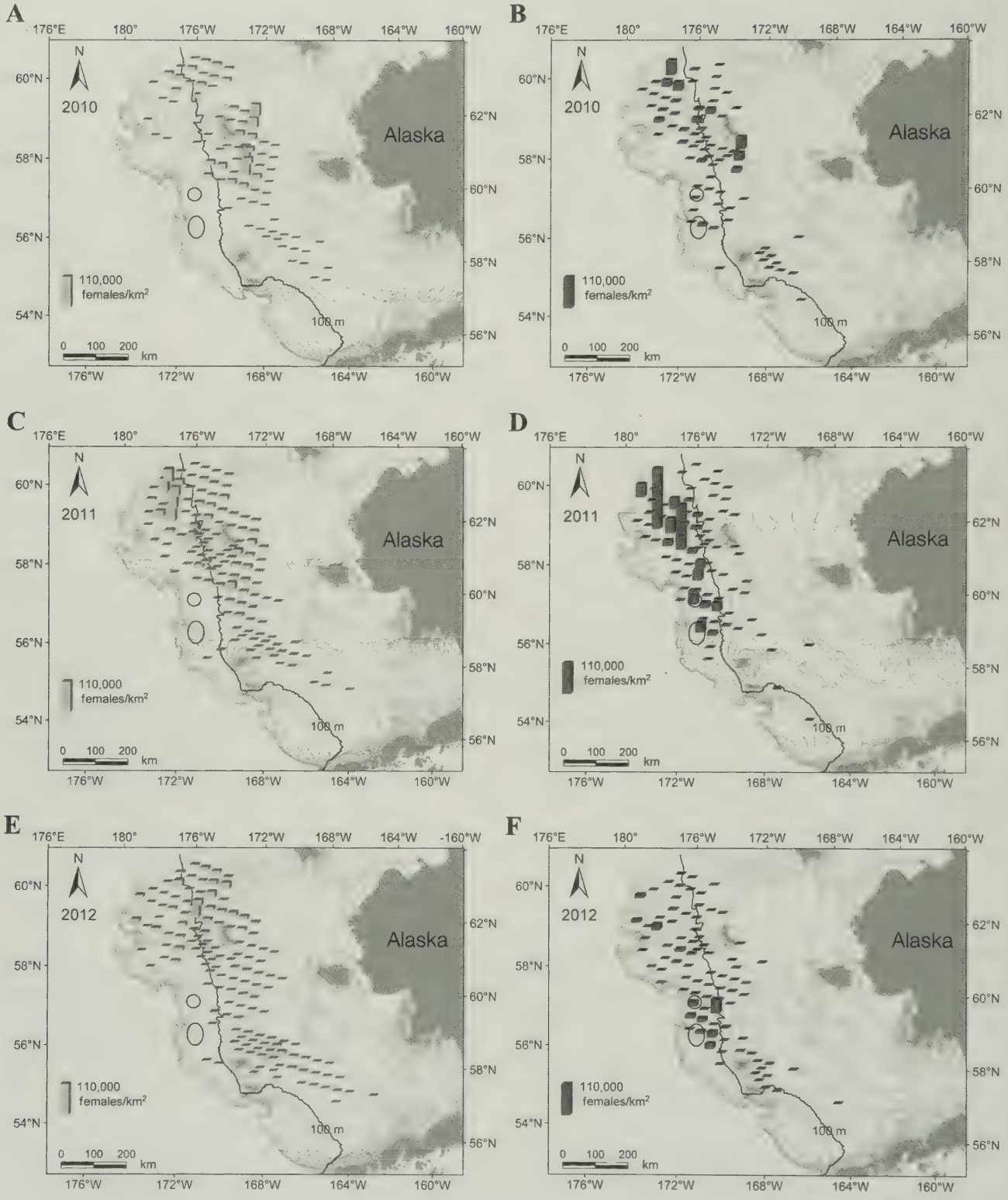

Figure 5

Summer distributions of primiparous female snow crabs (*Chionoecetes opilio*) during (**A**) 2010, (**C**) 2011, and (**E**) 2012 and of multiparous females during (**B**) 2010, (**D**) 2011, and (**F**) 2012, determined from data collected from the National Marine Fisheries Service summer bottom trawl surveys of the eastern Bering Sea. Bar heights indicate the catch per unit of effort (number of females per square kilometer). Ellipses indicate the tag release locations of morphometrically mature males. The black line indicates the 100-m bottom-depth contour, designating the approximate border between the middle and outer shelves.

offshore (Fig. 7B), as well as adolescent (small-clawed) males (Fig. 7F).

Regardless of the extent of inshore migrations among tagged MM males, most males traversed depths at which multiparous females resided, therefore, creating the potential for multiparous mating. Assuming that observed multiparous summer distributions do not differ significantly from their distributions during spring, when most of the multiparous mating occurs (Rugolo[2]), we conclude that there was broad spatial overlap between large MM males and multiparous females over the outer shelf during the mating period. In contrast, it is highly unlikely that pubescent-primiparous females mated with large older-shell MM males because of the lack of spatial overlap. Even for the 2 small tagged males that migrated to a depth of 90 m, a cross-shelf distance of approximately 100 km, the period when they occupied the shallowest waters occurred well after pubescent-primiparous mating (February–March; Ernst et al., 2005).

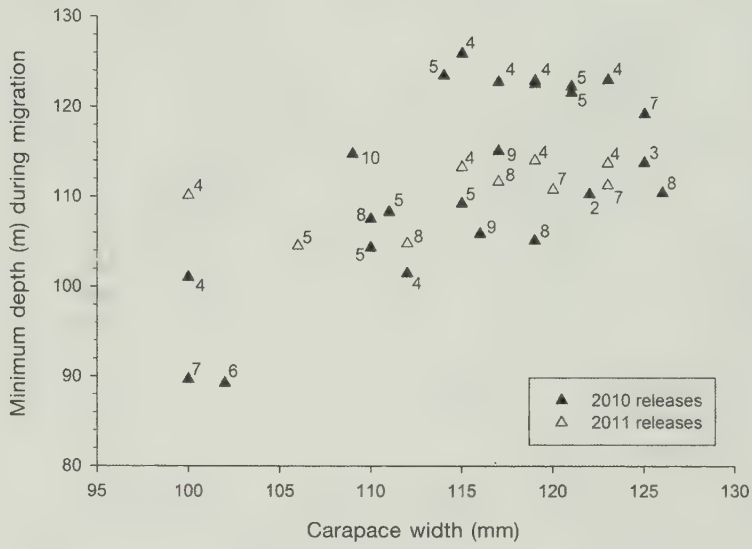

Figure 6

Relationship between the extent of inshore migrations and carapace widths of tagged morphometrically mature snow crabs (*Chionoecetes opilio*) released in the eastern Bering Sea in 2010 and 2011 (n=33). Inshore migration extent is defined as the minimum depth (y-axis) recorded while a tagged male was at liberty. Numbers next to the symbols indicate the month during which tagged males reached their minimum depth.

The reasons why 2 of the small tagged males migrated such long distances are debatable, particularly if a reason is related to mating because these males reached their shallowest water depth during June and July when multiparous mating is almost over. Still, an argument can be made that, because some multiparous females were still in a receptive condition during June and July (Chilton et al., 2011), the small tagged MM males underwent more extensive inshore migrations to breed with these females and avoid competition from large MM males. The exclusion of small MM males by large MM males during mating has been observed for snow crabs in waters of eastern Canada (Moriyasu and Comeau, 1996; Sainte-Marie et al., 1997; Comeau et al., 1998) as well as for southern Tanner crabs in the laboratory (Paul et al., 1995). Lovrich et al. (1995) documented the inshore movement of 60–68-mm-CW MM male snow crabs from the Gulf of St. Lawrence, and they interpreted this movement as a migration of these males early in the season (December) in order that they could mate with pubescent-primiparous females when there was no competition from large MM males. They also reported that some intermediate-size (~85 mm CW) MM males migrated inshore later in the season (May), the presumption being that they would mate with multiparous females while benefiting from reduced competition. As reported here, Lovrich et al. (1995) found that large MM males underwent some inshore movement during spring, but generally remained in deeper waters to mate with multiparous females.

A potential extension to this argument is that the 2 small tagged males engaged in grasping and carrying behavior (i.e., precopulatory embrace) and carried multiparous females from the main multiparous mating area to shallower waters, again, to reduce mating competition from larger MM males. Paired springtime migrations reportedly occur among snow crabs in Bonne Bay, Newfoundland, where MM males carry multiparous females from deeper to shallower waters (i.e., over a depth range from 150 to 10 m) for mating (Taylor et al., 1985; Hooper, 1986; Ennis et al., 1990; Comeau et al., 1991). In these studies, the peak of inshore multiparous spawning and mating occurred later in the season than the multiparous spawning and mating that occurred in deeper waters (Ennis et al., 1990), perhaps lending support to the idea of late inshore multiparous spawning and mating in the eastern Bering Sea.

That the 2 small tagged males in this study were among the earliest to migrate inshore (i.e., to make a 20-m depth change) during the first month after release in April, followed by more gradual inshore movement into June and July (Fig. 2A), could be interpreted as males initially migrating earlier than the other males to pick among the receptive multiparous females, and as males subsequently migrating slower with a female in grasp. Such a scenario, however, is still hypothetical considering the long distances (>100 km) migrated and that the interpreted periods of grasping and carrying (>2 months) are longer than those reported in the literature (Sainte-Marie et al., 2008).

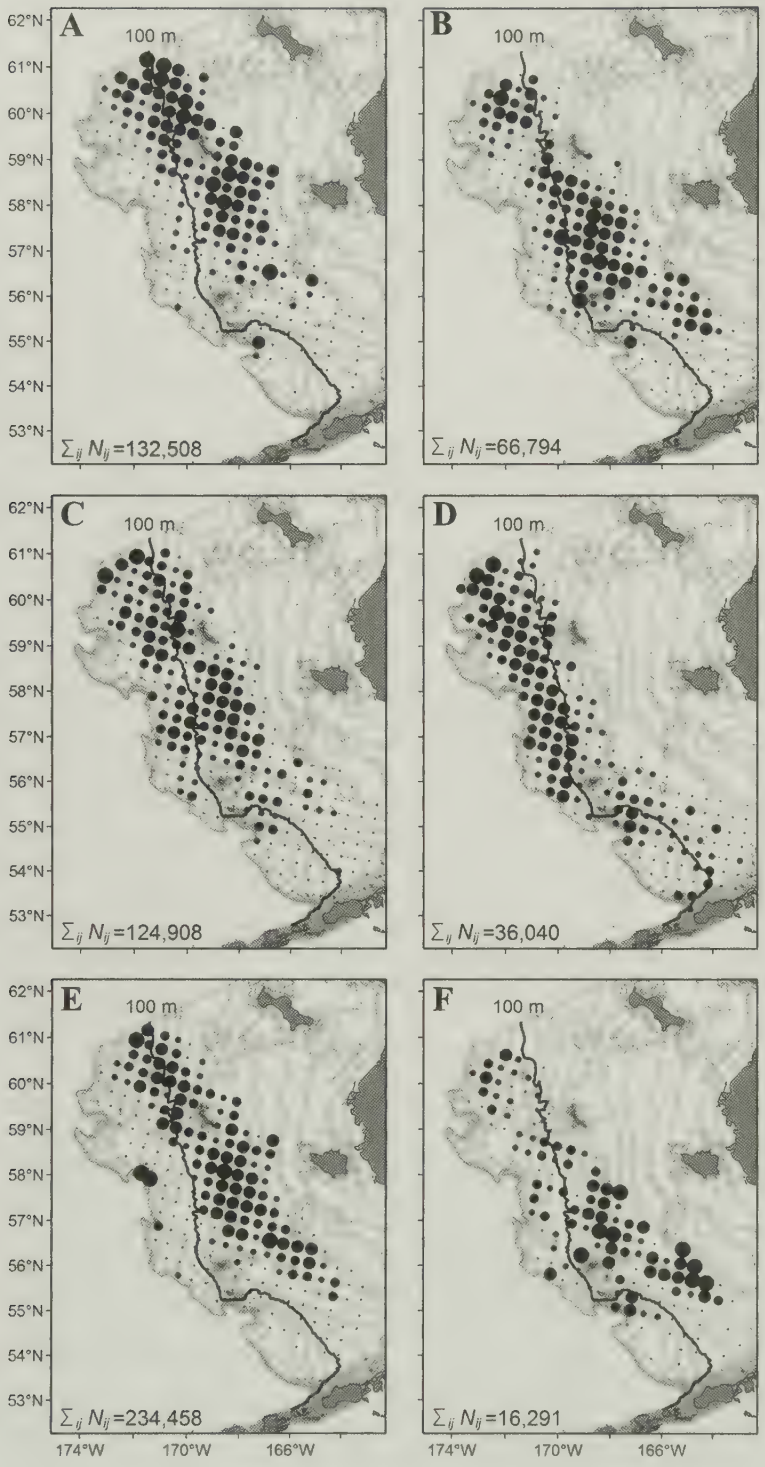

Figure 7

Distributions of morphometrically mature (MM; large-clawed) and adolescent (small-clawed) male snow crabs (*Chionoecetes opilio*) in the eastern Bering Sea during July, based on data collected annually (and pooled across years; 1989–2011) during National Marine Fisheries Service summer bottom trawl surveys. Distributions are classified within 4 categories of males: (**A**) small (70–100 mm in carapace width [CW]) males with new-shell condition (**B**) large (>100 mm CW) males with new-shell condition, (**C**) small males with older-shell condition, and (**D**) large males with older-shell condition. Distributions of adolescent males are classified by (**E**) small (70–100 mm CW) and (**F**) large (>100 mm CW) size classes. Relative abundance at each station was quantified as the proportion of MM males at each station in relation to MM males summed over all stations for all years. Dot sizes represent the following proportion ranges from smallest to largest: <0.002; 0.002–0.004; 0.004–0.008; 0.008–0.020; >0.020. Values of $\Sigma_{ij} N_{ij}$ are the sum of males captured at all stations i for all years j. The black line indicates the 100-m bottom-depth contour.

Assuming, on the basis of the data from DSTs, that large commercial-size MM males do not migrate inshore far enough, or soon enough, to mate with pubescent-primiparous females, the most likely partners for pubescent-primiparous mating were small (70–100 mm CW) MM males. Adolescent males from the Gulf of St. Lawrence have been found to mate with pubescent-primparous females in the laboratory (Moriyasu and Conan[6]; Sainte-Marie and Lovrich, 1994; Sainte-Marie et al., 1997), but their reproductive contribution in the field was thought to be limited (Sainte-Marie et al., 1999; Sainte-Marie et al., 2008). Instead, small MM males were found to be the primary partners of pubescent-primiparous females (Sainte-Marie and Hazel, 1992). It is not known if MM males <100 mm CW in the eastern Bering Sea undergo seasonal migrations, but given their close proximity to primiparous females during summer (Figs. 5 and 7C), they were the most readily available group of males to mate with these females.

Differences in the male–female mating dynamics of snow crabs from the eastern Bering Sea and those from eastern Canada are likely. Opportunities for different mating associations among the various reproductive stages (e.g., pubescent-primiparous and multiparous females and adolescent and MM males) could be greater in areas of steep bathymetry, for example, as a result of shorter migratory distances (Sainte-Marie et al., 2008) and related energetic costs (Foyle et al., 1989). The eastern Bering Sea shelf is flatter and wider than the Gulf of St. Lawrence. Because snow crabs are distributed along depth and temperature gradients according to their size and reproductive stage, the physical separation of these different groups may be greater over the eastern Bering Sea shelf than over the Gulf of St. Lawrence. Despite the geo-

[6] Moriyasu, M., and G. Y. Conan. 1988. Aquarium observation on mating behavior of snow crab, *Chionoecetes opilio*. ICES Council Meeting (C.M.) Documents 1986/K:9, 21 p. [Available at website.]

graphic differences, however, migration habits among large MM males in the 2 regions appear to be quite similar. In both locations, large MM males migrate to deeper water after their terminal molts (Ernst et al., 2005), make limited seasonal migrations back inshore, overlap the distribution of mature multiparous females during the spring mating season, and exhibit size dependence in regard to migration distance.

Assuming that large MM males seasonally migrate for the purpose of mating, we believe the extent and timing of their migrations is likely to depend on both the distribution of mature females and the seasonal timing of their reproductive cycle. Snow crab distributions have been shown to contract northward after years of warmer bottom temperatures (e.g., 1975–1979; Orensanz et al., 2004), and to shift back to the south (Turnock and Rugolo[4]) after a series of more recent colder-than-average years (2007–2010) and more extensive cold pools (Stabeno et al., 2012). The tagged MM males in this study were, therefore, at liberty during a relatively cold period. As indicated in this study, multiparous females were in close proximity to the tagged males, but perhaps, when waters are warmer, a shift in male and female distributions may necessitate longer migrations for mating. Colder temperatures also delay seasonal embryo hatching (Moriyasu and Lanteigne, 1998; Webb et al., 2007) and consequently subsequent mating, and therefore may result in earlier occurrence of migrations during warmer years.

Although the tagging data indicate timed migrations across depth gradients, and therefore inshore and offshore movements, we could not resolve movements that may have occurred along depth isobaths and therefore could not describe distinct migration routes for individuals. Another limitation of our study is that, although data from the NMFS bottom trawl surveys provided a clear pattern for the summer distribution of mature females, we did not have similar information collected during the mating period. Similarly, the distributional data for small MM males was limited to summer samples, and their overlap (or lack of) with tagged males during other seasons could not be determined. Additionally, although broad-scale distributional differences were found among adolescent and MM males of different size classes and with different shell conditions, annual differences in their distributions could not be determined because of a lack of annual CH–CW data needed to differentiate between adolescent and MM males. This shortcoming highlights the need for more comprehensive annual CH–CW collections.

Because of the lack of a substantial inshore migration of large MM males, it is important to recognize the component of the population targeted by the fishery and the impact of the fishery on female mating dynamics and reproductive success. Because large commercial-size MM males remain on the outer shelf, the existence of a summer–winter spatial difference among large males (including adolescents) on the outer shelf must, in part, be due to the annual removal of MM males by the fishery. The highest concentrations of commercial-size males observed during the NMFS summer bottom trawl survey in 2010 were found near the Pribilof Islands on the middle shelf (Turnock and Rugolo[4]), but our tag recoveries do not indicate that this finding is a result of migration of commercial-size MM males. Instead, these males must have been recently terminally molted MM males (i.e., new shell males) that had yet to migrate offshore, as well as adolescents. Again, considering what appears to be low relative abundance of large MM males on the outer shelf during summer, there must be some level of large MM male depletion during winter, and the winter fishery must be largely dependent on the annual recruitment of these new-shell MM males to the outer shelf.

Because of significant removals of commercial-size MM males by the fishery on the outer shelf, female spawners could become more reliant on either small MM males or adolescent males for mating (see Ennis et al., 1990). As stated earlier, because pubescent-primiparous females reside on the middle shelf, they are likely to mate with small resident MM males. For multiparous females, which reside on the outer shelf, their likely mates are the large MM males targeted by the fishery. However, because the fishery in the eastern Bering Sea typically occurs from January through March, just before multiparous mating (~March–July), the capture of large MM males would exclude them from multiparous mating. Considering that recently terminally molted males cannot mate for perhaps 3 months (Conan and Comeau, 1986; Paul et al., 1995; Sainte-Marie et al., 1999), even those large recently molted males that survive the fishery may not contribute to multiparous mating that year.

Of concern here, other than the reliance of the fishery on only one pseudocohort (individuals that terminally molted in the same year; see Ernst et al., 2005), is whether the male sperm contribution to spawning is sufficient in terms of both quantity and quality. Are the numbers of mature males that remain after fishery harvesting abundant enough to provide the sperm reserves necessary for healthy clutch fertilization and subsequent robust populations? Preliminary research on spermathecal loads among primiparous and multiparous females in the eastern Bering Sea has shown that they were significantly lower than those of females in the Gulf of St. Lawrence (Rugolo et al.[1]; Slater et al., 2010). Although there was no evidence of sperm limitation within the eastern Bering Sea stock, there is still a concern that the stock could be vulnerable to recruitment overfishing that results from reliance on a male-only fishery. The question remains, do multiparous females then become more reliant on stored sperm from pubescent-primiparous mating that occurred before their own offshore migration, or do they become more reliant on sperm from small, noncommercial-size MM males (e.g., Ennis et al., 1988; 1990) and potentially bias the genetic pool

toward smaller terminal sizes (Elner and Beninger, 1995; Tamone et al., 2005; Sainte-Marie et al., 2008)? Reduced reproductive output from multiparous females could place greater reliance upon mating and spawning of pubescent-primiparous females, which are known to have a lower fecundity (Haynes, et al., 1976; Sainte-Marie, 1993). Because multiparous mating is important for long-term sustainability of the snow crab in the eastern Bering Sea, it is important to ensure that adequate numbers of large MM males survive each year.

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Literature cited

Bowers, F. R., M. Schwenzfeier, K. Herring, M. Salmon, J. Shaishnikoff, H. Fitch, J. Alas, and B. Baechler.
2011. Annual management report for the commercial and subsistence shellfish fisheries of the Aleutian Islands, Bering Sea and the westward region's shellfish observer program, 2009/10. Alaska Dep. Fish Game, Fish. Manage. Rep. 11-05, 254 p. [Available at website.]

Chilton, E. A., C. E. Armistead, and R. J. Foy.
2011. The 2010 eastern Bering Sea continental shelf bottom trawl survey: Results for commercial crab species. NOAA Tech. Memo. NMFS-AFSC-216, 139 p.

Conan, G. Y., and M. Comeau.
1986. Functional maturity and terminal molt of male snow crab, *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci. 43:1710–1719.

Comeau, M., and G. Y. Conan,
1992. Morphometry and gonad maturity of male snow crab, *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci. 49:2460–2468.

Comeau, M., G. Robichaud, M. Starr, J.-C. Therriault, and G. Y. Conan.
1998. Mating of snow crab *Chionoecetes opilio* (O. Fabricius, 1788) (Decapoda, Majidae) in the fjord of Bonne Bay, Newfoundland. Crustaceana 71:925–941.

Comeau, M., G. Y. Conan, G. Robichaud, and A. Jones.
1991. Life history patterns and population fluctuations of snow crab (*Chionoecetes opilio*) in the fjord of Bonne Bay on the west coast of Newfoundland, Canada – from 1983 to 1990. Can. Tech. Rep. Fish. Aquat. Sci. 1817, 73 p.

Elner, R. W., and P. G. Beninger.
1995. Multiple reproductive strategies in snow crab, *Chionoecetes opilio*: physiological pathways and behavioral plasticity. J. Exp. Mar. Biol. Ecol. 193:93–112.

Ennis, G. P., R. G. Hooper, and D. M. Taylor.
1988. Functional maturity in small male snow crabs (*Chionoecetes opilio*). Can. J. Fish. Aquat. Sci. 45:2106–2109.
1990. Changes in the composition of snow crab (*Chionoecetes opilio*) participating in the annual breeding migration in Bonne Bay, Newfoundland. Can. J. Fish. Aquat. Sci. 47:2242–2249.

Ernst, B., J. M. Orensanz, and D. A. Armstrong.
2005. Spatial dynamics of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. Can. J. Fish. Aquat. Sci. 62:250–268.

Foy, R. J., and C. E. Armistead.
2013. The 2012 eastern Bering Sea continental shelf bottom trawl survey: results for commercial crab species. NOAA Tech. Memo. NMFS-AFSC-242, 147 p.

Foyle, T. P., R. K. O'Dor, and R. W. Elner.
1989. Energetically defining the thermal limits of the snow crab. J. Exp. Biol. 145:371–393.

Gutierrez, A.
2012. Opilio catch picks up just in time for a fast finish. Pacific Fish. 33:22.

Gravel, K. A., L. J. Watson, D. Pengilly.
2006. The 2005 eastern Bering Sea snow crab *Chioecetes opilio* tagging study. Alaska Dep. Fish Game, Fish. Manage. Rep. 06-31, 41 p. [Available at website.]

Haynes, E., J. F. Karinen, J. Watson, and D. J. Hopson.
1976. Relation of number of eggs and egg length to carapace width in the brachyuran crabs *Chionoecetes bairdi* and *C. opilio* from the southeastern Bering Sea and *C. opilio* from the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33:2592–2595.

Hooper, R. G.
1986. A spring breeding migration of the snow crab, *Chionoecetes opilio* (*O. Fabr.*), into shallow water in Newfoundland. Crustaceana 50:257–264.

Kotwicki, S., and R. R. Lauth.
2013. Detecting temporal trends and environmentally-driven changes in the spatial distribution of bottom fishes and crabs on the eastern Bering Sea shelf. Deep Sea Res. (II Top. Stud. Oceanogr.) 94:231–243.

Kruse, G. H., A. V. Tyler, B. Sainte-Marie, and D. Pengilly.
2007. A workshop on mechanisms affecting year-class strength formation in snow crabs (*Chionoecetes opilio*) in the eastern Bering Sea. Alaska Fish. Res. Bull. 12:278–291. [Available at website.]

Lauth, R. R.
2011. Results of the 2010 eastern and northern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate fauna. NOAA Tech. Memo. NMFS-AFSC-227, 256 p.

Lauth, R. R., and D. G. Nichol.
2013. Results of the 2012 eastern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate resources. NOAA Tech. Memo. NMFS-AFSC-256, 162 p.

Lovrich, G. A., B. Sainte-Marie, and B. D. Smith.
1995. Depth distribution and seasonal movements of *Chionoecetes opilio* (Brachyura: Majidae) in Baie Sainte-Marguerite, Gulf of Saint Lawrence. Can. J. Zool. 73:1712–1726.

Moriyasu, M. and M. Comeau.
1996. Grasping behavior of male snow crab *Chionoecetes opilio* (O. Fabricius, 1788) (Decapoda, Majidae). Crustaceana 69:211–222.

Moriyasu, M. and C. Lanteigne.
1998. Embryo development and reproductive cycle in the snow crab, *Chionoecetes opilio* (Crustacea:Majidae), in the southern Gulf of St. Lawrence, Canada. Can. J. Zool. 76:2040–2048.

Orensanz, J., B. Ernst, D. A. Armstrong, P. Stabeno, and P. Livingston.
2004. Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: an environmental ratchet? CalCOFI Rep. 45:65–79. [Available at website.]

Otto, R. S.
1998. Assessment of the eastern Bering Sea snow crab, *Chionoecetes opilio*, stock under the terminal molt hypothesis. *In* Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management (G. S. Jamieson and A. Campbell, eds.), p. 109–124. Can. Spec. Publ. Fish. Aquat. Sci. 125.

Parada, C., D. A. Armstrong, B. Ernst, S. Hinkley, and J. M. Orensanz.
2010. Spatial dynamics of snow crab in the eastern Bering Sea—putting together the pieces of the puzzle. Bull. Mar. Sci. 86:413–437.

Paul, A. J., J. M. Paul, and W. E. Donaldson.
1995. Shell condition and breeding success in Tanner crabs. J. Crust. Biol. 15:476–480. [Available at website.]

Sainte-Marie, B.
1993. Reproductive cycle and fecundity of primiparous and multiparous female snow crab, *Chionoecetes opilio*, in the northwest Gulf of Saint Lawrence. Can. J. Fish. Aquat. Sci. 50:2147–2156.

Sainte-Marie, B., T. Gosselin, J.-M. Sévigny, and N. Urbani.
2008. The snow crab mating system: opportunity for natural and unnatural selection in a changing environment. Bull. Mar. Sci. 83:131–161.

Sainte-Marie, B. and F. Hazel.
1992. Moulting and mating of snow crabs, *Chionoecetes opilio* (O. Fabricius), in shallow waters of the northwestern Gulf of Saint Lawrence. Can. J. Fish. Aquat. Sci. 49:1282–1293.

Sainte-Marie, B., and G. A. Lovrich.
1994. Delivery and storage of sperm at first mating of female *Chionoecetes opilio* (Brachyura: Majidae) in relation to size and morphometric maturity of male parent. J. Crust. Biol. 14:508–521. [Available at website.]

Sainte-Marie, B., and C. Carrière.
1995. Fertilization of the second clutch of eggs of snow crab, *Chionoecetes opilio*, from females mated once or twice after molt to maturity. Fish. Bull. 93:759–764.

Sainte-Marie, B., J.-M. Sévigny, and Y. Gauthier.
1997. Laboratory behavior of adolescent and adult males of the snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) mated noncompetitively and competitively with primiparous females. Can. J. Fish. Aquat. Sci. 54:239–248.

Sainte-Marie, N. Urbani, J.-M. Sévigny, F. Hazel, and U. Kuhnlein.
1999. Multiple choice criteria and the dynamics of assortative mating during the first breeding season of female snow crab *Chionoecetes opilio* (Brachyura, Majidae). Mar. Ecol. Prog. Ser. 181:141–153.

Slater, L. M., K. A. MacTavish, and D. Pengilly.
2010. Preliminary analysis of spermathecal load of primiparous snow crab (*Chionoecetes opilio*) from the eastern Bering Sea, 2005–2008. *In* Biology and management of exploited crab populations under climate change: 25th Lowell Wakefield Fisheries Symposium; Anchorage, AK, 10–13 March 2009 (G. H. Kruse, G. L. Eckert, R. J. Foy, R. N. Lipcius, B. Sainte-Marie, D. L. Stram, and D. Woodby, eds.), p. 237–247. Univ. Alaska Fairbanks, Alaska Sea Grant College Program Rep. AK-SG-10-01.

Somerton, D. A.
1981. Life history and population dynamics of two species of Tanner crab, *Chionoecetes bairdi* and *C. opilio*, in the eastern Bering Sea with implications for management of the commercial harvest. Ph.D. diss., 220 p. Univ. Wash., Seattle.
1982. Bipartite breeding: a hypothesis of the reproductive pattern in Tanner crabs. *In* Proceedings of the international symposium on the genus *Chionoecetes*; Anchorage, AK, 3–6 May (B. Melteff, ed.), p. 283–289. Univ. Alaska Fairbanks, Alaska Sea Grant Rep. AK-SG-82-10.

Stabeno, P. J., N. B. Kachel, S. E. Moore, J. M. Napp, M. Sigler, A. Yamaguchi, and A. N. Zerbini.
2012. Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep Sea Res. (II Top. Stud. Oceanogr.) 65:31–45.

Stevens, B. G., W. E. Donaldson, J. A. Haaga, and J. E. Munk.
1993. Morphometry and maturity of paired Tanner crab, *Chionoecetes bairdi*, from shallow- and deepwater environments. Can. J. Fish. Aquat. Sci. 50:1504–1516.

Tamone, S. L., M. M. Adams, and J. M. Dutton.
2005. Effect of eyestalk-ablation on circulating ecdysteroids in hemolymph of snow crabs, *Chionoecetes opilio*: physiological evidence for a terminal molt. Integr. Comp. Biol. 45:166–171.

Tamone, S. L., S. J. Taggart, A. G. Andrews, J. Mondragon, and J. K. Nielsen.
2007. The relationship between circulating ecdysteroids and chela allometry in male Tanner crabs: evidence for a terminal molt in the genus *Chionoecetes*. J. Crust. Biol. 27:635–642. [Available at website.]

Taylor, D. M., R. G. Hooper, and G. P. Ennis.
1985. Biological aspects of the spring breeding migration of snow crabs, *Chionoecetes opilio*, in Bonne Bay, Newfoundland (Canada). Fish. Bull. 83:707–711.

Webb, J., and J. Bednarski.
2010. Variability in reproductive potential among exploited stocks of Tanner crab (Chionoecetes bairdi) in southeast Alaska. *In* Biology and management of exploited crab populations under climate change: 25th Lowell Wakefield Fisheries Symposium; Anchorage, AK, 10–13 March 2009 (G. H. Kruse, G. L. Eckert, R. J. Foy, R. N. Lipcius, B. Sainte-Marie, D. L. Stram, and D. Woodby, eds.), p. 295–317. Univ. Alaska Fairbanks, Alaska Sea Grant College Program Rep. 10-01.

Webb, J. B., G. L. Eckert, T. C. Shirley, and S. L. Tamone.
2007. Changes in embryonic development and hatching in *Chionoecetes opilio* (snow crab) with variation in incubation temperature. Biol. Bull. 213:67–75.

Zheng, J., G. H. Kruse, and D. R. Ackley.
2001. Spatial distribution and recruitment patterns of snow crabs in the eastern Bering Sea. *In* Spatial processes and management of marine populations (G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, and D.Witherell, eds.), p. 233–255. Univ. Alaska Fairbanks, Alaska Sea Grant College Program AK-SG-01-02.

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Effects of oyster harvest activities on Louisiana reef habitat and resident nekton communities

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Abstract—Oysters are often cited as "ecosystem engineers" because they modify their environment. Coastal Louisiana contains extensive oyster reef areas that have been harvested for decades, and whether differences in habitat functions exist between those areas and nonharvested reefs is unclear. We compared reef physical structure and resident community metrics between these 2 subtidal reef types. Harvested reefs were more fragmented and had lower densities of live eastern oysters (*Crassostrea virginica*) and hooked mussels (*Ischadium recurvum*) than the nonharvested reefs. Stable isotope values (^{13}C and ^{15}N) of dominant nekton species and basal food sources were used to compare food web characteristics. Nonpelagic source contributions and trophic positions of dominant species were slightly elevated at harvested sites. Oyster harvesting appeared to have decreased the number of large oysters and to have increased the percentage of reefs that were nonliving by decreasing water column filtration and benthopelagic coupling. The differences in reef matrix composition, however, had little effect on resident nekton communities. Understanding the thresholds of reef habitat areas, the oyster density or oyster size distribution below which ecosystem services may be compromised, remains key to sustainable management.

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Ecologists have long recognized the importance of "ecosystem engineers" in organizing and maintaining ecosystems through their modification of the availability of resources in the environment (Jones et al., 1994, 1997). Oysters are commonly acknowledged as ecosystem engineers of shallow-water estuaries. Oysters modify the local environment by providing refuge and foraging habitat (Peterson et al., 2003; Coen et al., 2007), by altering local hydrodynamic processes (Lenihan, 1999), and by affecting local water quality (Newell et al., 2005; Piehler and Smyth, 2011; zu Ermgassen et al., 2013). Globally, more than 85% of oyster reefs have been identified as functionally extinct; disease, poor water quality, and destruction of the physical habitat have been identified as the major proximate causes (Beck et al., 2011). More specifically, the loss of vertical relief and complexity of oyster reefs, largely a result of commercial harvesting, is often cited as the primary factor that drives reef decline (Rothschild et al., 1994; Kirby, 2004).

Changes in the physical structure of reefs through natural processes, such as storm events or human activities associated with harvest, may affect the habitat value of reefs by altering refuge availability and reef community structure (Breitburg, 1999; Soniat et al., 2004; Humphries et al., 2011a). Alteration of the physical structure of reefs directly affects nekton populations by changing the availability of potential habitat, and several studies have highlighted the cascading effects of altered reef properties on trophic dynamics within an oyster reef community (Lenihan et al., 2001; Grabowski and Powers, 2004; Grabowski et al., 2008). Other studies have highlighted the impacts of reduced biomass of oysters, or other filter feeding organisms, on ambient water quality (Cloern, 1982; Fulford et al., 2007; zu Ermgassen et al., 2013).

More than 40% of the commercial production of the eastern oyster (*Crassostrea virginica*) in the continental United States occurs in coastal Louisiana estuaries (LDWF[1]), and oysters are the dominant reef-form-

[1] LDWF (Louisiana Department of Wildlife and Fisheries). 2012. Oyster stock assessment report of the public oyster areas in Louisiana: seed grounds and seed reservations. Oyster Data Rep. Ser. 18, 88 p. [Available from Louisiana Dep. Wildl. Fish., P.O. Box 98000, Baton Rouge, LA 70898.]

ing organism within these estuaries. Harvest activities occur across large areas of oyster reefs (LDWF[1]), but the effects of harvest and management on resident nekton communities, reef structure, and trophic interactions have yet to be quantified. Reefs in this region are characterized as largely subtidal, located in a microtidal, well-mixed environment, and have limited vertical relief (<50 cm). Therefore, the effects of harvesting on reefs in Louisiana may not be evident in large-scale changes in vertical relief but may be observed more in oyster density and size and in alteration of the reef matrix; oyster density and size, and alteration of the reef matrix may in turn affect refuge value and filtration capacity of an oyster reef (e.g., Summerhayes et al., 2009; La Peyre et al., 2014a).

We compared reef physical structure and resident community metrics on commercially harvested and nonharvested oyster reefs in coastal Louisiana. We quantified and characterized the abundance and composition of the resident nekton community at these oyster reefs. These data were examined to determine whether any differences in resident nekton community structure could be attributed to changes in reef characteristics. Lastly, using stable isotope analyses, we examined whether differences in reef characteristics were associated with differences in food web dynamics, such as the contributions of basal food sources, trophic level, and niche breadth of abundant resident organisms.

Materials and methods

Study area

This study was conducted on subtidal reefs located in estuarine shallow-water areas of coastal Louisiana. The coastal bays and estuaries in Louisiana are microtidal (tidal range: <1 m), and most water depths were within a range of 1–4 m. Oyster reefs are located in mid-salinity (salinity range=5–25) areas within the extensive salt and brackish marsh regions of the Louisiana coast and tend to cover large, heterogeneous areas. The reefs are often extensive and unmapped, and, therefore, they are difficult to delineate. We selected paired harvested and nonharvested sites, all located within similar salinity zones and on public oyster seed grounds that are managed by the Louisiana Department of Wildlife and Fisheries (LDWF[2], 2010; Fig. 1). For this study, harvest activities included removal of oysters for harvesting, as well as management activities, such as deposition of cultch (i.e., shell and limestone) to provide recruitment substrate. Nonharvested reefs were areas where it has been illegal to harvest oysters for several decades.

Two sites, Sabine Lake and northern Calcasieu Lake, have been closed to harvesting activities for more than 50 years, and they are the only substantial nonharvested subtidal oyster reefs in the state. There is no evidence that cultch deposition has occurred at these sites in the last 50 years. The sites were initially closed for health concerns that no longer persist, and over the last 5 years, there has been enormous pressure to open these areas to harvest. The remaining 2 areas, southern Calcasieu Lake and Sister Lake, are actively harvested with dredges. The most recent cultch deposition in these areas occurred on southern Calcasieu Lake in 2009 (0.06 km^2 of no. 57 limestone), and on Sister Lake in 2009 (0.63 km^2 of no. 57 limestone).

Sites were paired on the basis of ecological similarity and not proximity. The sites of northern and southern Calcasieu Lake were sampled as 1 pair; these 2 sites are located within the same waterbody and experience similar salinity regimes (long-term mean salinity: 13.9–16.1) and storm events. Sabine Lake and Sister Lake were paired because of similarities in salinity regimes (long-term mean salinity: 11.9–15.1) and water depths, and both sites are considered interior, large, shallow waterbodies. Although these 2 sites were farther apart from one another geographically than the other paired sites, the assumption was made that if harvest causes significant effects on the habitat, differences that result from harvest activities would be greater than differences associated with actual coastal location.

Data collection

Field data Reefs were located within each site with side-scan sonar data (ENCOS[3]) for Sabine, Southern Calcasieu, and Sister lake sites and with GPS coordinates from a planting of oyster shell cultch in 1969 for northern Calcasieu Lake. At each of the 4 sites, 3 sample stations, measuring 10 m×10 m, were established on reef habitat located more than 100 m from the marsh edge and in the centers of reef areas to remove confounding effects of adjacent habitats and reef edge (Fig. 2; Acosta and Robertson, 2002; Grabowski et al., 2005). At each sample station, reef structure, water quality, and resident nekton communities were sampled according to protocols listed below. All sample stations in Sabine Lake and Sister Lake were sampled twice during summer (July–August) 2010, and all sample stations in northern and southern sites in Lake Calcasieu were sampled twice during fall (September–October) 2010.

For each summer sampling event, 3 replicate samples per station were taken (with trays, which are described in the next section); because of high tray loss in the summer, 4 replicate samples were taken per sample station for each fall sampling event to increase

[2] LDWF (Louisiana Dep.Wildl. Fish.). 2010. Oyster stock assessment report of the public oyster areas in Louisiana: seed grounds and seed reservations. Oyster Data Rep. Ser. 16, 92 p. [Available at website.]

[3] ENCOS. 2008. Water bottom assessment of selected portions of public oyster seed grounds within Cameron Parish, Louisiana: Calcasieu and Sabine Lakes, 391 p. Prepared for the Louisiana Dep. Wildl. Fish. [Available from Louisiana Dep. Wildl. Fish., P.O. Box 98000, Baton Rouge, LA 70898.]

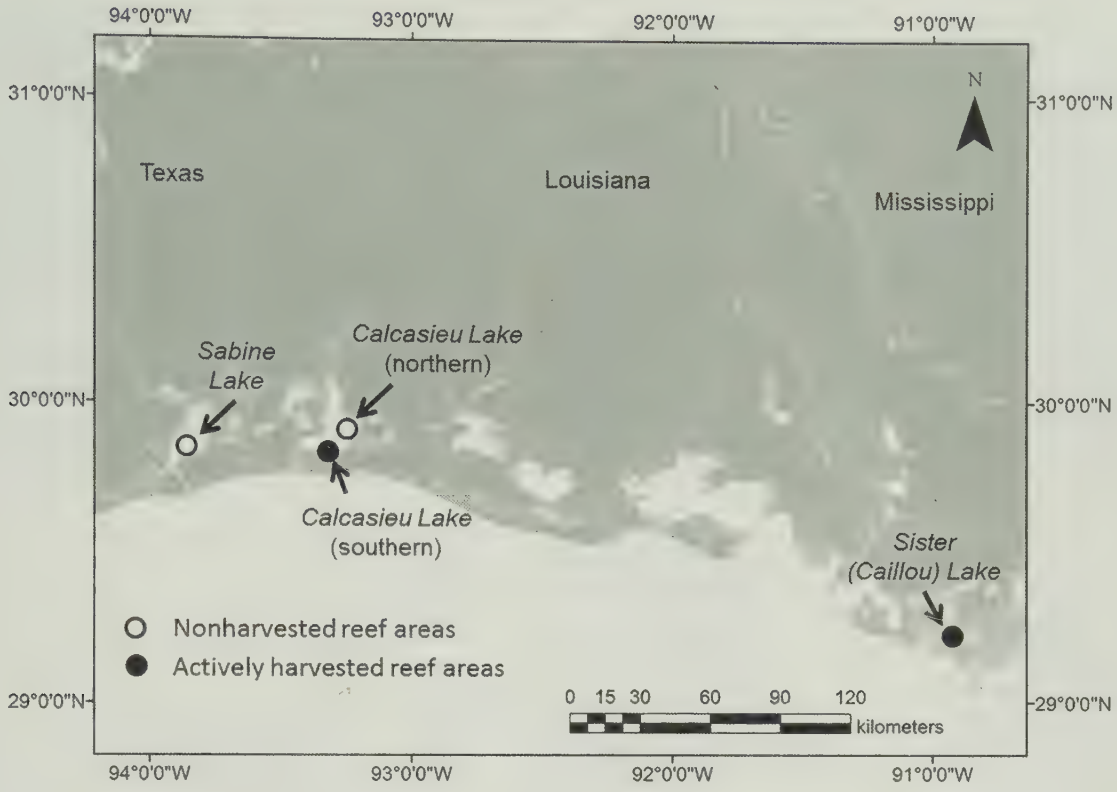

Figure 1

Map of the locations of the 4 sites, Sabine Lake, Sister Lake, and northern and southern Calcasieu Lake, in coastal Louisiana where data were collected in 2010 to describe oyster reef characteristics and associated resident reef community.

the number of trays successfully retrieved (for summer sites: 2 treatments×3 sample stations×3 trays×2 sample events=36 samples planned; for fall sites: 2 treatments×3 sample stations×4 trays×2 sample events=48 samples planned).

Resident nekton Resident nekton were sampled by using a benthic sample tray with an added mesh drawstring bag that was pulled closed before tray retrieval to prevent escape of mobile organisms. Trays are frequently used to sample oyster reef residents (Lehnert and Allen, 2002; Yeager and Layman, 2011) because of the impracticality of using nets to capture the cryptic species that live within the complex oyster reef matrix. Trays consisted of 0.22-m^2 plastic trays (0.47 m×0.47 m×0.08 m), which had their sides and bottoms lined with 3-mm mesh (Fig. 3). At deployment, trays were filled with local oyster reef substrate collected with a small dredge at adjacent reefs more than 100 m from sampling stations and with the amount needed to displace 5.0 L of water volume. The volume of 5.0 L was chosen because it completely fills the tray with substrate.

Deployment times ranged from 1 to 3 weeks because weather affected our ability to retrieve the trays. Lehnert and Allen (2002) and others have found that tray soak times of 2–7 days were adequate for sampling resident nekton at subtidal oyster shell habitats and that the communities recruited to trays did not change significantly after 7 days.

Upon retrieval, all organisms were collected, placed on ice, and taken to the laboratory, where they were identified with the use of field guides to the lowest practical taxon (Felder, 1973; Thompson, 1986; Hopkins et al, 1987; Hoese and Moore, 1998; Kells and Carpenter, 2011), measured (total length in millimeters for fish and shrimp, carapace width in millimeters for crabs, and wet-weight in grams), and frozen at a temperature of −20°C. If a tray was dumped during retrieval (i.e., some tray contents were lost because of improper net function), organisms were still collected and identified for possible use during stable isotope analyses but were not included in species abundance comparisons. All data for densities of organisms are reported as the number of individuals per square meter.

Reef structure Reef composition was determined by counting and measuring material placed in each tray before deployment. Volume of loose shells and shell clusters was measured by water displacement. Shell clusters were defined as having a minimum of 3 fused oyster shells. The volume of loose shells and clusters provides a proxy for the availability of small and large

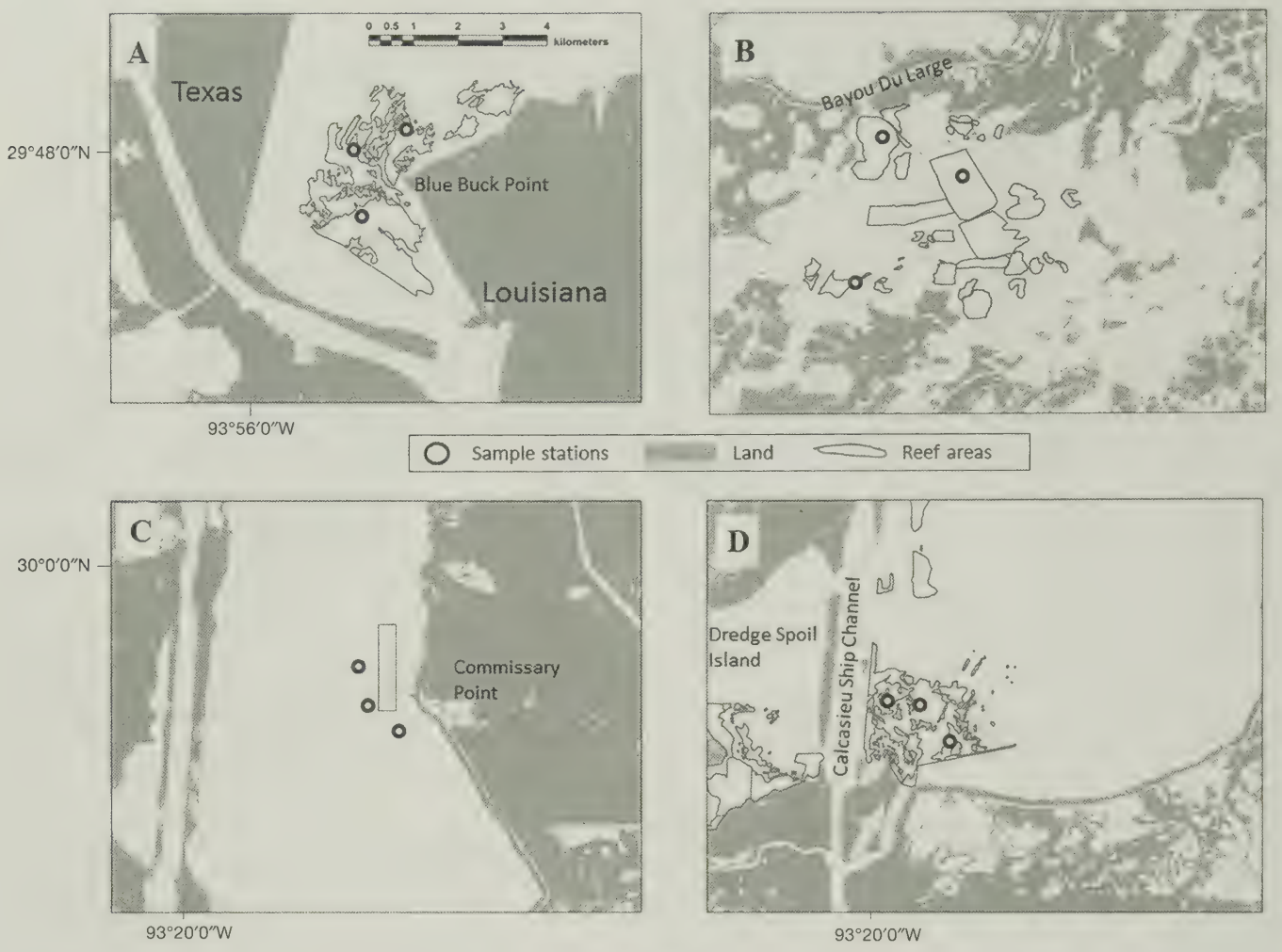

Figure 2

Maps of the locations of the 3 stations (○) at each of 4 sites in coastal Louisiana where resident reef communities and reef structure were sampled in 2010: (**A**) Sabine Lake, (**B**) Sister Lake, (**C**) northern Calcasieu Lake, and (**D**) southern Calcasieu Lake. All reef areas were determined from sonar data, except the reef area in northern Calcasieu Lake, which is based on only GPS coordinates for the footprint of a cultch planting in 1969. The sites at Sabine and Sister lakes were sampled in summer 2010 with 3 samples per station; the northern and southern sites at Calcasieu Lake were sampled in fall 2010 with 4 samples per station.

interstitial reef space, respectively. Total numbers of oysters, of market-size oysters (shell height: >75 mm), and of seed oysters (shell height: 25–75 mm) were counted. At tray retrieval, the number of hooked mussels (*Ischadium recurvum*) within 1.0 L of substrate per tray was counted as an indicator of settlement of other (nonoyster) sessile organisms.

Reef integrity and vertical relief were estimated at each sample station. To estimate reef integrity (percentage of area that consisted of solid reef), 20 haphazard measurements were taken by quickly tapping the bottom of the seafloor twice with a long pole and recording the bottom type (solid, mixed shell and mud, or mud). Solid reef was assigned a value of 1.0, mixed shell and mud was assigned a value of 0.5, and mud was assigned a value of 0.0. An index of integrity was calculated by adding the assigned values and dividing by 20. To measure vertical relief, 20 haphazard depth measurements were taken at each station. The difference between the 2 extreme depth measures was used as an index of vertical relief.

Water quality Upon retrieval of each nekton sampling tray, dissolved oxygen (DO; measured as milligrams per liter), salinity, and temperature (measured in degrees Celsius) data were collected at each sample station at the surface (~10 cm below the surface) and the bottom (~10 cm above the bottom) of the water column with a YSI Model 85[4] multiparameter sensor (YSI, Inc., Yellow Springs, OH). One surface water sample was collected

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the U.S. government.

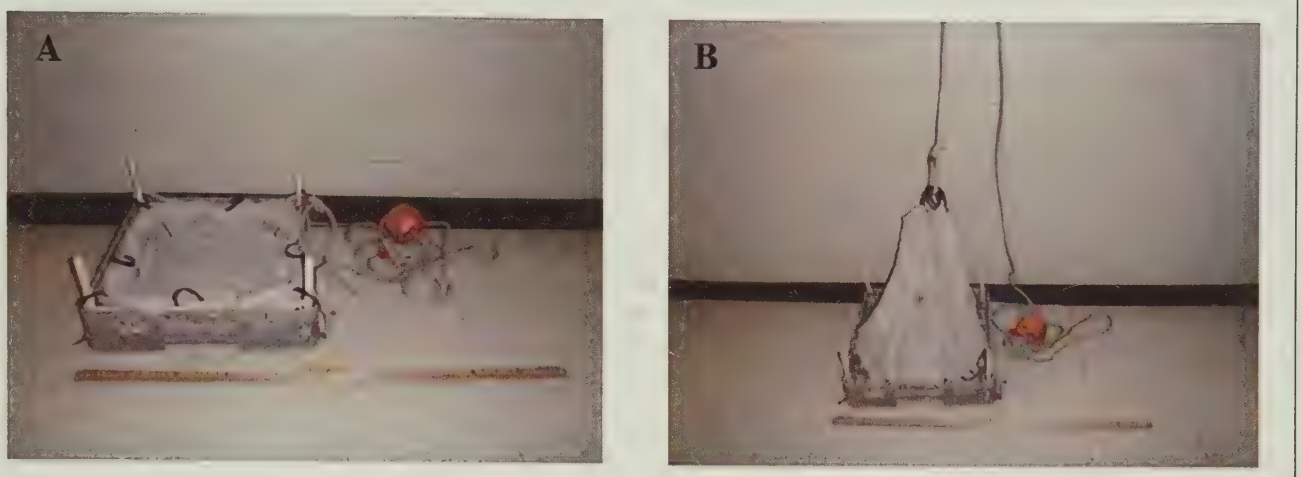

Figure 3

The modified sample tray used for sampling resident communities of oyster reefs in 2010 in coastal Louisiana, showing (**A**) the mesh drawstring as it would be when deployed and (**B**) the mesh drawstring pulled for tray retrieval.

at each station with a 250-mL, opaque Nalgene bottle, placed on ice, taken to the laboratory, and immediately analyzed for chlorophyll-*a* (measured in micrograms per liter) (Arar[5]) and total particulate matter (TPM; measured in milligrams per liter) (Rice et al., 2012).

Isotope samples

Sample collection Resident organisms used for stable isotope analyses were taken from tray samples. For each species found across all sites, only organisms of similar size were used in order to remove any effects of ontogenetic dietary shifts; organisms had to be combined across stations to obtain adequate numbers of each species from each site. Organisms collected included the eastern oyster, hooked mussel, the flatback mud crab (*Eurypanopeus depressus*), grass shrimp (*Palaemonetes* spp.), the naked goby (*Gobiosoma bosc*), the freckled blenny (*Hypsoblennius ionthas*), and the skilletfish (*Gobiesox strumosus*). Adductor muscle tissue was used for eastern oysters, and the entire organism was used for hooked mussels (excluding their shells), flatback mud crabs, and grass shrimp. Tail portions were used for naked goby and skilletfish samples, and epaxial muscle tissue was used for freckled blenny.

Samples of basal food sources were collected at each site: fine particulate organic matter (FPOM; <200 µm, pelagic source) and dominant marsh plants (nonpelagic, detrital source). For FPOM samples, a 1-L bottle of water was collected from each station (3 samples per site), filtered through 200-µm mesh, and placed on ice. Three samples clipped from the stems of the marsh plant (*Spartina* spp.) were collected (20 m apart from each other) from each site and placed on ice. Coarse particulate organic matter (CPOM; >200 µm) was collected with a ring-net plankton tow (3-string bridle, 50-cm diameter) fitted with 200-µm mesh, pulled at each station for 2 min at a speed of 2.6 m/s (5 kn). Plankton tow contents were placed in a 1-L opaque bottle after visible detritus were removed and these bottles were placed on ice and taken to the laboratory for content analysis. FPOM and CPOM samples were filtered through Whatman glass microfiber filters (GF/F, precombusted for 3 h at 450°C) until flow was obstructed, and the filters with the filtrate were frozen at –20°C.

Sample preparation and analyses

All samples were dried to a constant weight at 60°C, they ground to a powder, and treated to remove lipids. Inorganic carbonates were removed from shrimp, crabs, FPOM, and CPOM through treatment with minute quantities of 1N hydrochloric acid until the reaction ceased (Jacob et al., 2005). Lipids were extracted in 2 separate 24-h decantations with hexane at room temperature (Fry et al., 2003). Once they were treated for lipids and inorganic carbonates, samples were placed back into a drying oven at 60°C until they reached a constant weight. Faunal tissue samples of 1 mg (standard error [SE] 0.2) and plant tissue samples of 2–3 mg were weighed for stable isotope analyses. For filtered FPOM and CPOM samples, a small portion cut from the center of the filter was used for analyses. All samples were analyzed for $\delta^{15}N$ and $\delta^{13}C$ by the University of California Stable Isotope Facility with a PDZ Europa ANCA-GSL elemental analyzer (Sercon, Ltd.,

[5] Arar, E. J. 1997. Method 446.0: *In vitro* determination of chlorophylls a_1, b_1, $c_1 + c_2$ and pheopigments in marine and freshwater algae by visible spectrophotometry, rev 1.2, 26 p. National Exposure Research Laboratory, Office of Research and Development, U. S. Environmental Protection Agency. [Available at website.]

Crewe, UK) interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon, Ltd.).

Data analyses

Field data Data on water quality, reef structure, and organism abundance (dependent variables) were analyzed separately by season. For all analyses, a significance level of alpha=0.05 was used, and results are presented as means with standard errors. Unless otherwise indicated, SAS software, vers. 9.2 (SAS Institute, Inc., Cary, NC) with the GLIMMIX procedure was used for all analyses. Data for water quality, reef structure, and resident oyster reef community were analyzed by using separate generalized linear mixed models (GLMMs) to test for the effects of harvesting (independent variable), with station used as a nested random effect to remove effects of station variation. Bottom DO, salinity, temperature, chlorophyll-*a*, TPM, water depth, and index of integrity were examined by harvesting treatment (actively harvested and nonharvested) with GLMMs that used station as a nested random effect to remove effects of station variation. To examine differences in depth and index of integrity, GLMMs were run with a normal distribution. Densities of market- and seed-size oysters, mussel density, volume of loose shells, and volume of shell clusters were also analyzed by harvest treatment with station as a nested random effect; in addition, a negative binomial distribution with a log-link function was used to account for overdispersion. Significant results for water quality and reef structure parameters were determined with a type-III test of fixed effects. Vertical relief for the 2 harvesting treatments was compared with a 2-sample *t*-test. Specifically, vertical relief, the difference between the 2 extreme depth measures, was calculated at each station, for 3 stations per site (N=6 [3 stations×2 sites]). For resident oyster reef communities, GLMMs with a negative binomial distribution and a log-link function to account for overdispersion were run on common species density (species representing >1% of total abundance), invertebrate density, fish density, total nekton density (fishes and invertebrates combined), and total number of species. Significant results for resident community parameters were determined with a type-III test of fixed effects.

For examination of species–environment relationships, canonical correspondence analysis (CCA) was performed with CANOCO software, vers. 4.5 (Wageningen UR, Netherlands; ter Braak and Smilauer, 2002) to analyze the relationship between abundances of common resident species and environmental variables (water quality and reef structure), by combining all summer and fall catches. Summer and fall catches were combined to increase the number of samples per species and to focus on species–environment relationships that held true, regardless of season. The number of environmental variables was reduced by using backward selection, sequentially removing the least influential variable until 4 variables remained. Species abundances were $\log(x+1)$ transformed for the CCA to improve normality. A Monte Carlo simulation test was used to determine statistical significance of canonical axes with 1000 simulations on the full model.

Stable isotope data Isotope data were analyzed by season. Isotope values of $\delta^{15}N$ to $\delta^{13}C$ were used to determine contributions of basal food sources (BFSs; marsh plant and FPOM) and consumer trophic positions (dependent variables). Contributions of BFSs to naked goby, freckled blenny, skilletfish, grass shrimp, flatback mud crabs, eastern oysters, and CPOM were determined for each site by using a 2-source mixing model (Fry, 2006), with the mean $\delta^{13}C$ values of dominant marsh plants and FPOM from each site. Trophic position (TP) was determined with the following equation:

$$TP = 1 + (\delta^{15}N_{Organism} - \delta^{15}N_{Base})/TEF \text{ (Post, 2002)},$$

where a trophic enrichment factor (TEF) of 2.54‰ was used (Vanderklift and Ponsard, 2003; Caut et al., 2009).

Separate 2 sample *t*-tests were used to test for differences between harvest treatments (independent variable) for the trophic position and BFS contributions of dominant species (Post, 2002; Layman et al., 2007). The convex hull area (the smallest area that incorporates all isotope biplot points for individual species or communities) were calculated and used as a means to represent the trophic diversity within a food web (Layman et al., 2007), but they were not statistically tested because there was only one set of convex hull areas per site (no replication). Convex hull areas were constructed with the convex hull option in the XTools Pro toolbar in ArcMap, the central application of ArcGIS, vers. 9.3.1 (Esri, Redlands, CA). Data for harvest treatments that were not normally distributed were compared with a nonparametric Wilcoxon rank-sum test.

Results

Field data

Water quality In the summer, there were no differences in temperature, salinity, and DO between harvested and nonharvested treatments (Table 1). Levels of TPM and chlorophyll-*a* were higher at the harvested site, Sister Lake (44.2 mg/L [SE 3.2] and 18.0 µg/L [SE 2.0]), than at the nonharvested site, Sabine Lake (17.9 mg/L [SE 3.5] and 8.2 µg/L [SE 0.4]).

In the fall, there were no differences in temperature or DO between harvest treatments (Table 1). Chlorophyll-*a* levels were higher at the harvested site, southern Calcasieu Lake (16.9 µg/L [SE 0.4]), than at the nonharvested site, northern Calcasieu Lake (8.6 µg/L [SE 0.3]). Salinity was significantly higher at the nonharvested site (20.0 [SE 0.2]) than at the harvested site (19.2 [SE 0.2]), although the difference was probably not ecologically important.

Table 1

Mean measurements of water quality and reef structure for sampled oyster reefs in Louisiana during summer and fall 2010. Degrees of freedom (df) for *F*-values are provided in parentheses and apply to all results except for reef vertical relief, for which df=2 and a 2-sample *t*-test was used to compare treatments. Significant differences ($P<0.05$) between harvest treatments are indicated with asterisks (*). Standard errors of the mean are provided in parentheses. NH=not harvested; AH=actively harvested.

	Summer				Fall			
Parameter	Sabine Lake (NH)	Sister Lake (AH)	*F*-value	*P*-value	North Calcasieu (NH)	South Calcasieu (AH)	*F*-value	*P*-value
Temperature (°C)	31.0 (0.2)	31.1 (0.2)	0.02	0.89	26.4 (0.8)	24.9 (1.1)	1.28	0.32
Salinity	13.0 (1.2)	12.0 (0.4)	0.56	0.49	20.0 (0.2)	19.2 (0.1)	12.53	0.024*
Dissolved oxygen (mg/L)	5.2 (0.3)	4.4 (0.3)	0.38	0.57	6.9 (0.1)	6.3 (0.2)	2.55	0.19
Total particulate matter (mg/L)	17.9 (3.5)	44.2 (3.2)	9.78	0.04*	75.6 (1.1)	90.2 (5.3)	6.36	0.07*
Chlorophyll-*a* (µg/L)	8.2 (0.4)	18.0 (2.0)	18.89	0.01*	8.6 (0.3)	16.9 (0.4)	244.88	<0.0001*
Cluster volume (L)	3.9 (0.1)	2.9 (0.2)	3.82	0.12	4.4 (0.1)	1.8 (0.1)	221.38	<0.0001*
Loose shell volume (L)	0.3 (0.1)	0.8 (0.2)	1.8	0.25	0	2.0 (0.1)	80.7	0.0008*
Reef integrity (unitless)	0.8 (0.1)	0.6 (0.1)	10.06	0.004*	0.9 (0.1)	0.8 (0.1)	4.52	0.04*
Reef depth (m)	2.6 (0.02)	1.9 (0.03)	10.58	0.03*	1.2 (0.01)	1.8 (0.01)	88.32	0.0007*
Reef vertical relief (m)	0.20 (0.00)	0.17 (0.03)	1.00 (df=2)	0.42	0.67 (0.03)	0.10 (0.00)	1.00 (df=2)	0.42
Total oyster density (no./tray)	67.0 (2.9)	114.8 (16.4)	0.83	0.41	70.5 (4.5)	20.7 (1.1)	131.22	0.0003*
Market size oyster density (no./tray)	32.3 (1.8)	9.2 (1.1)	40.54	0.003*	17.5 (0.4)	12.6 (0.7)	6.42	0.06
Seed size oyster density (no./tray)	34.7 (2.3)	101.5 (16.5)	2.02	0.23	43.1 (3.9)	6.0 (0.7)	58.12	0.0016*
Mussel density (no./tray)	636.4 (61.0)	319.2 (79.2)	2.39	0.2	1424.7 (22.5)	54.7 (5.7)	3724.47	<0.0001*

Reef structure In the summer, there were no differences in the volume of loose shells, shell clusters, vertical relief, total oyster density, seed oyster density, or mussel density (Table 1). Reef integrity, depth, and density of market-size oysters were lower at the harvested site (0.6 [SE 0.1], 1.9 m [SE 0.03], and 9.2 individuals/tray [SE 1.1], respectively) than at the nonharvested site (0.8 [SE 0.1], 2.6 m [SE 0.02], and 32.3 individuals/tray [SE 1.8], respectively).

In the fall, there were no differences in vertical relief or in density of market-size oysters (Table 1). Volume of shell clusters was higher at the nonharvested site than at the harvested site: 4.4 L (SE 0.1) versus 1.8 L (SE 0.1). Conversely, loose shell volume was higher at the harvested site than at the non-harvested site: 2.0 L (SE 0.1) versus 0.0 L (SE 0.0). Reef depth was greater at the harvested site than at the nonharvested site: 1.8 m (SE 0.01) versus 1.2 m (SE 0.01). Total oyster density, seed oyster density, and mussel density were higher at the nonharvested site (70.5 individuals/tray [SE 4.5], 43.1 individuals/tray [SE 3.9], 1424.7 individuals/tray [SE 22.5], respectively) than at the harvested site (20.7 individuals/tray [SE 1.1], 6.0 individuals/tray [SE 0.7], 54.7 individuals/tray [SE 5.7], respectively).

Nekton community In the summer, 14 tray samples were collected at the nonharvested site, and 12 tray samples were collected at the harvested site (48% tray retrieval success rate) for a total of 26 trays. Densities of naked goby and estuarine mud crabs (*Rhithropanopeus harrisii*) were higher at the harvested site (102.8 individuals/m^2 [SE 21.4], 20.1 individuals/m^2 [SE 6.3]) than at the nonharvested site (9.4 individuals/m^2 [SE 1.6], 0.7 individuals/m^2 [SE 0.4]) (Table 2). The number of invertebrate species and total number of species also were greater at the harvested site (5.5 individuals/m^2 [SE 0.4], 9.0 individuals/m^2 [SE 0.5]) than at the nonharvested site (3.4 individuals/m^2 [SE 0.2], 6.2 individuals/m^2 [SE 0.3]).

In the fall, 15 tray samples were collected at the nonharvested site, and 17 tray samples were collected at the harvested site (66% tray retrieval success rate) for a total of 32 trays. Densities of grass shrimp were greater at the nonharvested site, with a mean of 132.6 individuals/m^2 (SE 17.0) than at the harvested site, with a mean of 65.6 individuals/m^2 (SE 12.7) (Table 2). The number of fish species was also greater at the non-harvested site than at the harvested site: 2.5 individuals/m^2 (SE 0.2) versus 1.5 individuals/m^2 (SE 0.2).

Species environment The CCA indicated a significant relationship between nekton assemblage structure and environmental variables (P=0.001; Fig. 4). The horizontal axis, which explained 58.3% of the variation

Table 2

Mean species density (individuals/m^2), mean number of species captured, and *F*-values and *P*-values from generalized linear mixed models run, by site for species collected in summer and fall 2010 at actively harvested (AH) and nonharvested (NH) oyster reefs in Louisiana. Degrees of freedom for *F*-values are provided in parentheses. Significant differences ($P<0.05$) between harvest treatments are indicated by asterisks (*). Only species that contributed to more than 1% of the total catch were analyzed statistically. Note that *n* refers to the number of trays successfully sampled for abundance data. Standard errors of the mean are provided in parentheses.

	Summer				Fall			
Scientific name	Sabine Lake (NH) *n*=14	Sister Lake (AH) *n*=12	*F*(1, 4)	*P*-value	North Calcasieu Lake (NH) *n*=15	South Calcasieu Lake (AH) *n*=17	*F* (1, 4)	*P*-value
Gobiosoma bosc	9.4 (1.6)	102.8 (21.4)	19.26	0.01*	49.7 (6.2)	51.9 (2.8)	0.06	0.82
Hypsoblennius ionthas	7.8 (2.1)	18.2 (5.0)	0.08	0.8	1.5 (0.6)	0.8 (0.4)	0.27	0.63
Gobiesox strumosus	3.3 (0.9)	10.6 (2.9)	1.32	0.31	3.9 (0.9)	0.8 (0.6)	6.17	0.07
Chasmodes bosquianus	0.7 (0.4)	2.3 (1.0)			1.5 (0.6)	0.8 (0.4)		
Opsanus beta	3.3 (1.2)	1.5 (0.9)			0	0.3 (0.3)		
Myrophis punctatus	0	2.7 (1.6)			0	0		
Lutjanus griseus	0	0.4 (0.4)			0.6 (0.4)	0		
Chaetodipterus faber	0.3 (0.3)	0.4 (0.4)			0	0		
Gobionellus boleosoma	0.3 (0.3)	0.4 (0.4)			0	0		
Paralichthys lethostigma	0.3 (0.3)	0			0	0		
Fish density	25.4 (3.4)	139.2 (26.0)	10.17	0.03*	57.3 (6.2)	54.6 (2.8)	0.17	0.7
Number of fish species	2.8 (0.3)	3.5 (0.4)	1.16	0.34	2.5 (0.2)	1.5 (0.2)	11.69	0.03*
Eurypanopeus depressus	74.8 (12.1)	106.9 (15.3)	1.96	0.23	173.5 (17.9)	171.0 (14.3)	0.03	0.87
Palaemonetes spp.	207.7(28.8)	103.9 (36.3)	2.02	0.23	132.6 (17.0)	65.6 (12.7)	8.98	0.04*
Panopeus simpsoni	22.4 (2.8)	13.7 (2.7)	4.91	0.09	0.9 (0.7)	15.8 (2.4)	5.97	0.07
Callinectes sapidus	0	14.0 (5.2)	3.28	0.14	13.9 (4.2)	15.5 (5.2)	5.33	0.08
Rhithropanopeus harrisii	0.7 (0.4)	20.1 (6.3)	19.26	0.01*	0	0		
Alpheus heterochaelis	0.7 (0.4)	9.1 (2.6)			0.3 (0.3)	4.6 (1.7)		
Menippe adina	0.3 (0.3)	4.6 (1.3)			2.1 (0.8)	5.6 (1.4)		
Farfantepenaeus aztecus	0.3 (0.3)	1.5 (1.0)			0	0.8 (0.6)		
Petrolisthes armatus	0	0			0	0.3 (0.3)		
Clibanarius vittatus	0	0.8 (0.8)			0	0		
Invertebrate density	306.8 (29.8)	274.5 (37.8)	0.41	0.56	323.4 (22.9)	279.2 (22.3)	1.34	0.13
Number of invertebrate species	3.4 (0.2)	5.5 (0.4)	14.26	0.02*	3.2 (0.3)	3.4 (0.2)	4.87	0.09
Total density	332.2 (29.4)	413.7 (55.9)	0.1	0.77	380.7 (21.0)	333.8 (24.5)	1.82	0.25
Total number of species	6.2 (0.3)	9.0 (0.5)	23.9	0.008*	5.7 (0.3)	6.3 (0.3)	1.69	0.26

in nekton assemblage (eigenvalue=0.11), was highly correlated with reef integrity (coefficient of correlation [*r*]=–0.69) and distinguished species that prefer fragmented reef habitats. Species, such as the bigclaw snapping shrimp (*Alpheus heterochaelis*) and the estuarine mud crab, were associated with reefs with low integrity values (<50%). The vertical axis, which accounted for 27.7% of the variation (eigenvalue=0.05), was negatively associated with volume of loose shells (r=–0.70) and positively associated with total number of live oysters (r=0.70), and this axis distinguishes species that prefer live oyster habitats. Species, such as the freckled blenny (*H. ionthas*) and skilletfish, were strongly positively associated with the number of live oysters.

Stable isotopes

For the summer sampling, results from a 2-source mixing model indicated that pelagic basal food sources (i.e., FPOM) contributed more to the food web of the resident community on the sampled oyster reefs than the nonpelagic sources (i.e., marsh plant) regardless of harvest treatment (all values of source fractions of FPOM were >0.50; Table 3). The pelagic source contribution was higher for flatback mud crabs at the nonharvested site (0.65 [SE 0.03]) than at the harvested site (0.53 [SE 0.04]). The trophic positions of the hooked mussel, eastern oyster, grass shrimp, skilletfish, and naked goby were elevated at the harvested site compared to the nonharvested site (Fig. 5).

For the fall sampling, pelagic source contributions were also found to contribute more to the resident community food web than the nonpelagic sources at both harvested and nonharvested sites. Pelagic source contributions were elevated at the harvested site for all organisms except skilletfish. The trophic positions of all organisms were elevated at the harvested site, except that of eastern oysters.

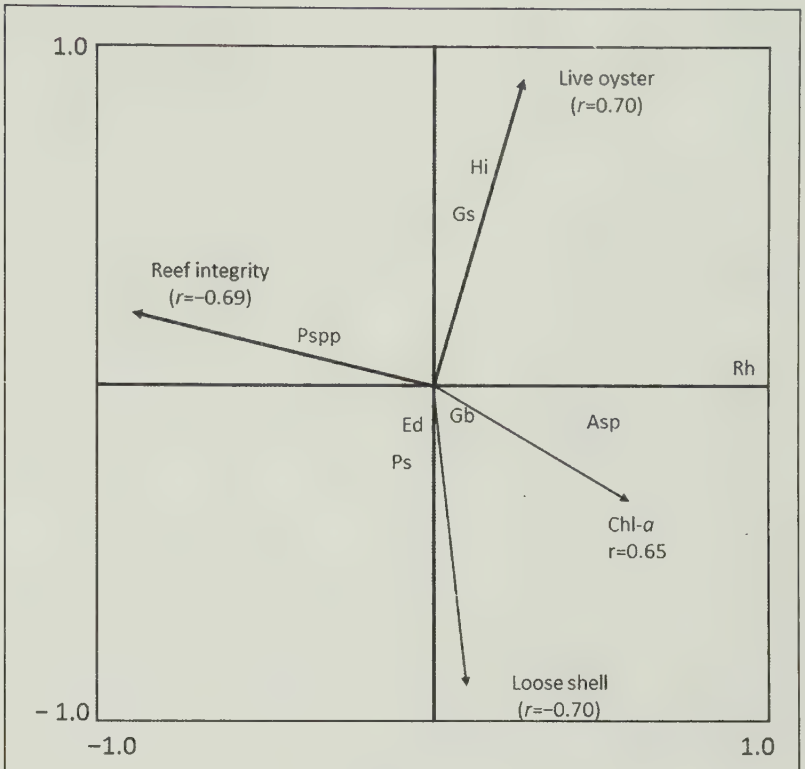

Figure 4

Canonical correspondence biplot relating species abundances with habitat variables at actively harvested and nonharvested oyster reefs of coastal Louisiana during 2010. The horizontal axis accounts for 58.3% of variation (eigenvalue: 0.11), and the vertical axis accounts for 27.7% of variation (eigenvalue: 0.05). Species abbreviations: Asp=bigclaw snapping shrimp (*Alpheus heterochaelis*), Ed=flatback mud crab (*Eurypanopeus depressus*, Gb=naked goby (*Gobiosoma bosc*), Gs =skilletfish (*Gobiesox strumosus*), Hi=freckled blenny (*Hypsoblennius Ionthas*), Ps=oystershell mud crab (*Panopeus Simpsoni*), Pspp=grass shrimp (*Palaemonetes* spp.), Rh= estuarine mud crab (*Rhithropanopeus harrisii*).

Discussion

Oyster reef structure, as defined by the extent of solid reef, number and size of live oysters, number of mussels, and interstitial space, can be substantially altered by oyster harvesting activities in coastal Louisiana. Such changes in reef structure did not translate into significant differences in the resident nekton community. Although harvested reefs were more fragmented and sometimes had fewer living oysters and mussels than nonharvested reefs, habitat use and food resources associated with the 2 types of reefs were similar. These results indicate that, although oyster harvest can change the composition of the reef matrix and alter habitat complexity, as long as adequate structural material is maintained, a reef provides suitable habitat for resident communities of small organisms.

Most models of reef degradation from harvest indicate that a loss of vertical relief and complexity lead toward increased stress on an oyster population and loss of oyster reef function (Rothschild et al., 1994; Lenihan and Peterson, 1998; Lenihan, 1999); however, we dealt with subtidal reefs with limited vertical relief. Vertical relief of all reefs in our study ranged from 10 to 20 cm, and reefs were located in depths of 1.2–2.9 m. Whether nonharvested reefs lacked relief because of degradation from historic activities or as a result of environmental constraints is unknown because of a lack of data from the early part of the 20th century.

In contrast with a lack of difference in vertical relief, harvested and nonharvested reefs differed substantially in the composition of reef matrix. As expected, more large live oysters, as well as less reef fragmentation and loose shells, were found at nonharvested sites than at the harvested reef areas. The lack of larger oysters at harvested reefs, a direct consequence of harvest activities, has been documented previously (Lenihan and Micheli, 2000; Lenihan and Peterson, 2004). The increase in fragmentation and loose shells at harvested sites may be dué to physical damage from a dredge or due to the frequent placement of shells as cultch by the Louisiana Department of Wildlife and Fisheries within the harvested sites (LDWF[2]). The combined effects of more loose shells, fewer shell clusters, and solid reef area may make the harvested reefs more susceptible to complete reef loss with overharvesting and with the scattering and sedimentation that occurs during storm events. However, as noted previously, flat reefs without small-scale changes in vertical relief are typical of this region. Many of these reefs have existed and been harvested since record keeping began around 1900.

Despite these differences in the oyster reef matrix, there were no consistent differences between treatments in the overall abundance or diversity of reef-associated nekton communities during fall and summer sampling. This lack of difference in nekton density at reefs with different physical and biological characteristics is similar to that found with other studies of artificial reefs of varying heights (Lenihan et al., 2001),

Table 3

Mean stable isotope values ($\delta^{13}C$ and $\delta^{15}N$), convex hull areas (CH), trophic position (TP), and mean basal food source contributions for dominant organisms collected on nonharvested reef (NH) and actively harvested (AH) oyster reefs in Louisiana during summer 2010 and fall 2010. F_{Marsh}=marsh plant (nonpelagic) source fraction; F_{FPOM}=fine particulate organic matter (pelagic) source fraction. Dominant organisms include coarse particulate matter (CPOM), hooked mussels (*Ischadium recurvum*), eastern oysters (*Crassostrea virginica*), flatback mud crab (*Eurypanopeus depressus*), grass shrimp (*Palaemonetes* spp.), skilletfish (*Gobiesox strumosus*), freckled blenny (*Hypsoblennius ionthas*), and naked goby (*Gobiosoma bosc*). Convex hull (CH) for the total community is also presented. Significant differences ($P<0.05$) in TP, F_{Marsh}, and F_{FPOM} between harvest treatments are indicated with asterisks (*). Standard errors of the mean are provided in parentheses. n=number of individual samples processed for each location.

	Sabine Lake (NH)							Sister Lake (AH)						
	n	$\delta^{13}C$	$\delta^{15}N$	CH	TP	F_{Marsh}	F_{FPOM}	n	$\delta^{13}C$	$\delta^{15}N$	CH	TP	F_{Marsh}	F_{FPOM}
Summer 2010														
Marsh plant	3	−12.81 (0.10)	7.09 (1.32)	–	–	–	–	3	−12.87 (0.07)	5.40 (0.54)	–	–	–	
FPOM	3	−28.94 (0.24)	7.31 (0.01)	–	–	–	–	3	−28.16 (0.20)	3.02 (1.44)	–	–	–	–
CPOM	3	−25.81 (0.62)	11.73 (0.54)	1.61	2.75 (0.22)	0.17 (0.04)	0.83 (0.04)	3	−24.51 (0.57)	10.82 (1.46)	3.55	3.77 (0.54)	0.24 (0.04)	0.76 (0.04)
I. recurvum	15	−25.69 (0.11)	8.99 (0.09)	1.15	1.68 (0.04)*	0.18 (0.01)	0.82 (0.01)	15	−24.83 (0.15)	6.94 (0.06)	0.57	2.30 (0.02)*	0.22 (0.01)	0.78 (0.01)
C. virginica	15	−23.70 (0.12)	11.54 (0.07)	0.92	2.69 (0.03)*	0.30 (0.01)	0.70 (0.01)	15	−23.20 (0.13)	9.36 (0.06)	0.70	3.13 (0.02)*	0.33 (0.01)	0.67 (0.01)
E. depressus	15	−21.03 (0.59)	11.60 (0.30)	13.34	2.73 (0.11)	0.47 (0.04)*	0.53 (0.04)*	15	−22.86 (0.43)	8.92 (0.16)	8.30	2.94 (0.06)	0.35 (0.03)*	0.65 (0.03)*
Palaemonetes spp.	15	−23.47 (0.16)	12.90 (0.15)	1.72	3.23 (0.06)*	0.31 (0.01)	0.69 (0.01)	15	−23.05 (0.11)	10.71 (0.14)	1.82	3.64 (0.05)*	0.33 (0.01)	0.67 (0.01)
G. strumosus	3	−21.93 (0.20)	13.88 (0.09)	0.10	3.62 (0.04)*	0.41 (0.01)	0.59 (0.01)	3	−22.17 (0.49)	11.89 (0.18)	0.06	4.04 (0.04)*	0.39 (0.03)	0.61 (0.03)
H. ionthas	3	−23.15 (0.30)	14.30 (0.24)	0.08	3.78 (0.10)	0.33 (0.02)	0.67 (0.02	3	−23.00 (0.18)	11.92 (0.25)	0.22	4.11 (0.10)	0.34 (0.01)	0.66 (0.01)
G. bosc	15	−23.12 (0.14)	14.51 (0.14)	2.08	3.87 (0.05)*	0.34 (0.01)	0.66 (0.01)	15	−22.86 (0.20)	12.03 (0.13)	1.57	4.14 (0.04)*	0.35 (0.01)	0.65 (0.01)
Community	–	–	–	29.5	–	–	–	–	–	–	25.24	–	–	–

	Northern Calcasieu Lake (NH)							Southern Calcasieu Lake (AH)						
	n	$\delta^{13}C$	$\delta^{15}N$	CH	TP	F_{Marsh}	F_{FPOM}	n	$\delta^{13}C$	$\delta^{15}N$	CH	TP	F_{Marsh}	F_{FPOM}
Summer 2010														
Marsh plant	3	−13.16 (0.21)	5.34 (0.28)	–	–	–	–	3	−13.35 (0.18)	6.64 (0.61)	–	–	–	–
FPOM	3	−24.97 (0.39)	5.47 (0.88)	–	–	–	–	3	−26.04 (1.13)	4.19 (2.95)	–	–	–	–
CPOM	3	−23.83 (0.21)	11.42 (0.98)	1.08	3.34 (0.39)*	0.10 (0.02)*	0.90 (0.02)*	3	−23.22 (0.42)	14.71 (0.32)	0.69	4.78 (0.12)*	0.22 (0.03)*	0.78 (0.03)*
I. recurvum	15	−23.97 (0.08)	9.17 (0.07)	0.60	2.46 (0.03)	0.08 (0.01)	0.92 (0.01)	0	–	–	–	–	–	–
C. virginica	15	−22.54 (0.08)	11.64 (0.20)	1.83	3.44 (0.08)	0.21 (0.01)*	0.79 (0.01)*	15	−20.49 (0.08)	12.01 (0.08)	0.66	3.56 (0.03)	0.44 (0.01)*	0.54 (0.01)*
E. depressus	15	−21.61 (0.50)	11.42 (0.13)	6.81	3.36 (0.05)*	0.28 (0.04)*	0.72 (0.04)*	15	−20.66 (0.30)	12.50 (0.12)	2.64	3.76 (0.06)*	0.42 (0.02)*	0.58 (0.02)*
Palaemonetes spp.	15	−21.31 (0.18)	12.91 (0.21)	4.40	3.94 (0..08)*	0.31 (0.02)*	0.69 (0.02)*	15	−20.08 (0.09)	13.87 (0.08)	0.73	4.24 (0.03)*	0.47 (0.01)*	0.53 (0.01)*
G. strumosus	3	−21.03 (0.07)	13.40 (0.17)	0.05	4.14 (0.07)*	0.33 (0.01)	0.67 (0.01)	3	−19.85 (0.07)	14.91 (0.09)	0.01	4.61 (0.04)*	0.49 (0.01)	0.51 (0.01)
H. ionthas	3	−21.67 (0.22)	13.70 (0.16)	0.18	4.25 (0.06)*	0.28 (0.02)*	0.72 (0.02)*	3	−20.12 (0.12)	15.16 (0.11)	0.01	4.73 (0.03)*	0.47 (0.01)*	0.53 (0.01)*
G. bosc	15	−21.56 (0.06)	14.42 (0.18)	0.99	4.54 (0.07)*	0.29 (0.01)*	0.71 (0.01)*	15	−19.87 (0.07)	15.77 (0.08)	0.74	4.94 (0.03)*	0.49 (0.01)*	0.51 (0.01)*
Community	–	–	–	24.05	–	–	–	–	–	–	15.63	–	–	–

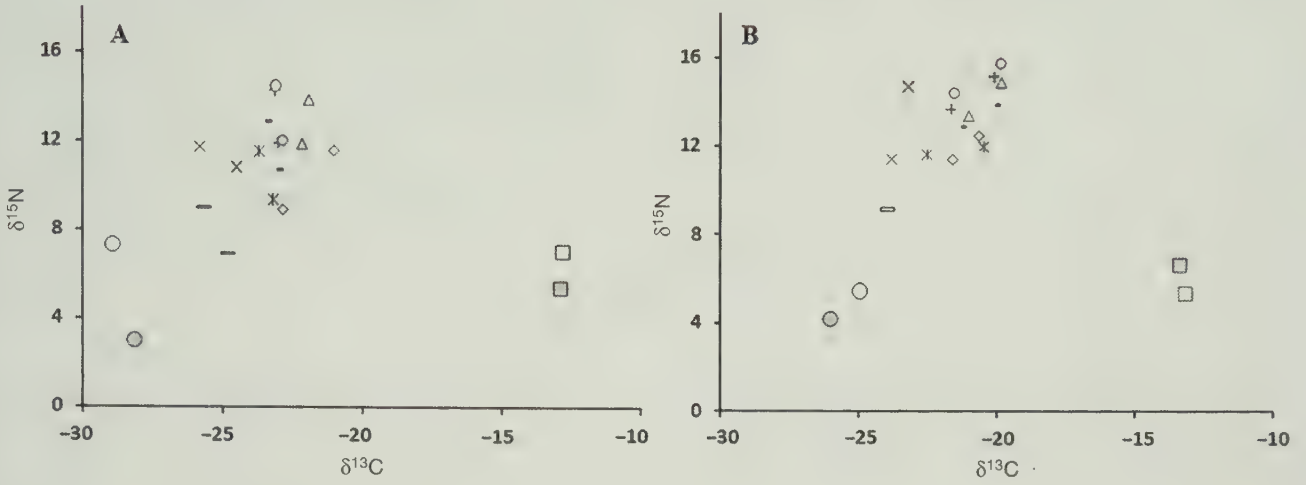

Figure 5

Biplot of mean $\delta^{13}C$ and $\delta^{15}N$ values of basal food sources and dominant faunal species sampled at 4 sites in coastal Louisiana in 2010: (**A**) Sabine Lake (nonharvested) and Sister Lake (actively harvested) in the summer and (**B**) northern (nonharvested) and southern (actively harvested) Calcasieu Lake in the fall. Error bars are omitted for simplicity; standard errors of the mean and sample sizes (*n*) are located in Table 3. Shaded symbols indicate means for harvested sites, and open symbols indicate means for nonharvested sites. Symbols for various organisms: large circle=fine particulate organic matter, square=marsh plant, ×=coarse particulate organic matter, large dash=hooked mussel (*Ischadium recurvum*), crossed ×=eastern oyster (*Crassostrea virginica*), diamond=flatback mud crab (*Eurypanopeus depressus*), short dash=grass shrimp (*Palaemonetes* spp.), triangle=skittlefish (*Gobiesox strumosus*), plus sign=freckled blenny (*Hypsoblennius ionthas*), and small circle=naked goby (*Gobiosoma bosc*).

shell density and vertical relief (Humphries et al., 2011b), and reefs with and without the presence of live oysters (Tolley and Volety, 2005; Summerhayes et al., 2009). Although ecological theory holds that structurally complex habitats are expected to sustain higher densities and more diverse communities than structurally simple ones, defining structural complexity has never been straightforward (Beck, 1998; Bartholomew et al., 2000), and it is not clear whether the harvested and nonharvested sites represented different levels of complexity or just differences in habitat characteristics. No consensus exists as to how to define oyster reef complexity; in some experiments oyster or shell density, vertical relief, or mixtures of unaggregated shells (simple) versus clusters (complex) were used, making it difficult to determine when complexity had actually changed (Grabowski and Powers, 2004; Grabowski et al., 2008; Humphries et al., 2011a).

The use of similar volumes of reef material in the trays may have contributed to the similarity of resident communities at our paired sites, but observed differences in the reef matrix may be important in determining preferred habitats of resident organisms. The use of 5.0 L of local reef substrate (an amount that corresponds to 22.7 L/m^2) to completely fill each sample tray may have resulted in densities of reef material that were beyond a threshold at which differences in nekton abundances can be noted (e.g., Humphries et al., 2011b). Samples obtained by diving on historic, created, and harvested reefs in the region have provided reef material sample volumes up to 11 L/m^2 in the top 10 cm of substrate (La Peyre et al., 2014b). The loose matrix of substrate material created by dredging and filling trays may have resulted in increased small interstitial spaces and elevated habitat availability.

Despite this potential criticism, tray substrate differences were observed between harvest treatments. The similarity of species diversity and community composition remains striking and indicates that the sampled harvested and nonharvested areas still support similar nekton communities, although specific niches for certain species were identified by apparent preferences for reef subhabitats. The CCA results indicate that the bigclaw snapping shrimp (*Alpheus heterochaelis*) and estuarine mud crab are associated with fragmented reef habitats exposed to high levels of chlorophyll-*a* and that the skilletfish and freckled blenny are associated with the presence of shell clusters (larger interstitial spaces) and high densities of live oysters.

Oysters are known to transfer nutrients from the water column to the benthos; however, the observed decrease in the number and size of live oysters at harvested sites, compared with the number and size at nonharvested sites, may have other trophic effects beyond a decrease in benthopelagic coupling. Filtration rate on a reef is generally held to increase with oyster biomass (Cloern, 1982; Officer et al., 1982; Dame, 1996). In our study, mean levels of chlorophyll-*a* at

harvested sites consistently were double the levels at nonharvested sites. The reduced number of large oysters and mussels combined with a probable reduction in overall numbers of other sessile filter-feeding organisms at harvested reefs may contribute to decreased filtration capacity (Dame et al., 1989; Cressman et al., 2003).

Resident communities at both types of oyster reefs appear to depend primarily on pelagic basal food sources (i.e., FPOM). The increase in the fractions of detrital source (i.e., marsh plant), combined with elevated chlorophyll-*a* levels, indicates a reduction in benthopelagic coupling services at harvested reefs. Benthic microalgae could also contribute to the food webs of oyster reef communities; however, in San Antonio Bay, Texas (also a shallow, turbid estuary), the microphytobenthos contributed less than 2% of the primary production found in the water column (MacIntyre and Cullen, 1996). Benthic macroalgae, seagrass epiphytes, and upstream terrestrial plant matter can also contribute to the basal food source (Abeels et al., 2012), but these sources were not observed within the studied reef areas.

Trophic position of resident organisms on harvested oyster reefs was slightly elevated in comparison with nonharvested reefs, but trophic order was maintained. Although deriving a TEF specific to these systems may result in different estimates of trophic positions, the trends observed would not change. Differences in trophic position of resident species have also been found between reefs and mud-bottom sites (Quan et al., 2012) and between reefs that were experiencing different riverine exposures (Abeels et al., 2012).

In these instances, trophic shifts may be attributed to increased infaunal diversity associated with combined mud and shell substrate or to increased phytoplankton abundance from riverine inputs. For example, there is evidence that a lower abundance of filter feeders may result in increased zooplankton abundance (Lonsdale et al., 2009) and potentially in a more diverse planktonic community. Elevated chlorophyll-*a* levels indicate increased phytoplankton abundance at harvested sites. Increased planktonic diversity or higher densities of top planktonic predators (ctenophores) could explain the increase in the trophic position of CPOM at harvested reefs. For the remainder of species, the maintenance of the trophic order for the 2 reef types and the lack of consistent difference in convex hull areas is an indication that the differences in the reef matrix between the harvested and nonharvested sites that were documented in this study did not result in significant changes in feeding behaviors, but the observed shifts in trophic positions and CCA results indicate that reef alteration may have affected the planktonic and infaunal forage base.

Changes in populations of oysters and in the biogenic reefs that these ecosystem engineers create are predicted to have effects on surrounding community structure and ecosystem processes. The results of this study indicate that, on the public oyster grounds in Louisiana, effects of harvesting are subtle for reef types in close proximity (northern and southern Calcasieu Lake) and for those across larger areas (Sabine and Sister lakes). Oyster harvesting practices that alter the reef matrix yet preserve live oysters and reef substrate may still provide important habitat for the resident nekton community. What has yet to be examined is whether there is a threshold of reef habitat area, oyster density, or oyster size distribution below which ecosystem services will be severely compromised.

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Literature cited

Abeels, H. A., A. I. Loh, and A. K. Volety.
2012. Trophic transfer and habitat use of oyster *Crassostrea virginica* reefs in southwest Florida, identified by stable istope analysis. Mar. Ecol. Prog. Ser. 462:125–142.

Acosta, C. A., and D. N. Robertson.
2002. Diversity in coral reef fish communities: the effects of habitat patchiness revisited. Mar. Ecol. Prog. Ser. 227:87–96.

Bartholomew, A., R. J. Diaz, and G. Cicchetti.
2000. New dimensionless indices of structural habitat complexity: predicted and actual effects on a predator's foraging success. Mar. Ecol. Prog. Ser. 206:45–58.

Beck, M. W.
1998. Comparison of the measeurment and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. Mar. Ecol. Prog. Ser. 169:165–178.

Beck, M. W., R. D. Brumbaugh, L. Airoldi, A. Carranza, L. D. Coen, C. Crawford, O. Defeo, G. J. Edgar, B. Hancock, M. C. Kay, H. S. Lenihan, M. W. Luckenbach, C. L. Toropova, G. Zhang, and X. Guo.
2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. Bioscience 61:107–116.

Breitburg, D. L.
1999. Are three-dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? *In* Oyster reef habitat restoration: a synopsis and synthesis of approaches (M. W. Luckenbach, R. Mann, and J. A. Wesson, eds), p.

239–250. Virginia Institute of Marine Science Press, Gloucester Point, VA.

Caut, S., E. Angulo, and F. Courchamp.
2009. Variation in discrimination factors (delta $\Delta^{15}N$ and delta $\Delta^{13}C$): the effect of diet isotopic values and applications for diet reconstruction. J. Appl. Ecol. 46:443–453.

Cloern, J. E.
1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? Mar. Ecol. Prog. Ser. 9:191–202.

Coen, L. D., R. D. Brumbaugh, D. Bushek, R. Grizzle, M. W. Luckenbach, M. H. Posey, S. P. Powers, and S. G. Tolley.
2007. Ecosystem services related to oyster restoration. Mar. Ecol. Prog. Ser. 341:303–307.

Cressman, K.A., M. H. Posey, M. A. Mallin, L. A. Leonard, and T. D. Alphin.
2003. Effects of oyster reefs on water quality in a tidal creek estuary. J. Shell. Res. 22:753–762.

Dame, R.F., J.D. Spurrier, and T.G. Wolaver.
1989. Carbon, nitrogen and phosphorus processing by an oyster reef. Mar. Ecol. Prog. Ser. 54:249–256.

Dame, R. F.
1996. Ecology of marine bivalves: an ecosystem approach, 272 p. CRC Press, Boca Raton, FL.

Felder, D. L.
1973. An annotated key to crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico. Louisiana Sea Grant Publ. LSU-SG-73-02, 103 p. Center for Wetland Resources, Louisiana State Univ., Baton Rouge, LA. [Available at website.]

Fry, B., D. M. Baltz, M. C. Benfield, J. W. Fleeger, A. Gace, H. L. Haas, and Z. J. Quiñones-Rivera.
2003. Stable isotope indicators of movement and residency of brown shrimp (*Farfantepenaeus aztecus*) in coastal Louisiana marshscapes. Estuaries 26:82–97.

Fry, B.
2006. Stable isotope ecology, 308 p. Springer Science+ Business Media, New York.

Fulford, R. S., D. L. Breitburg, R. I. E. Newell, W. M. Kemp, and M. Luckenbach.
2007. Effects of oyster population restoration strategies on phytoplankton biomass in Chesapeake Bay: a flexible modeling approach. Mar. Ecol. Prog. Ser. 336:43–61.

Grabowski, J. H., and S. P. Powers.
2004. Habitat complexity mitigates trophic transfer on oyster reefs. Mar. Ecol. Prog. Ser. 277:291–295.

Grabowski, J. H., A. R. Hughes, D. L. Kimbro, and M. A. Dolan.
2005. How habitat setting influences restored oyster reef communities. Ecology 86:1926–1935.

Grabowski, J. H., A. R. Hughes, and D. L. Kimbro.
2008. Habitat complexity influences cascading effects of multiple predators. Ecology 89:3413–3422.

Hoese, H. D., and R. H. Moore.
1998. Fishes of the Gulf of Mexico: Texas, Louisiana, and adjacent waters, 2nd ed., 422 p. Texas A&M Univ. Press, College Station, TX.

Hopkins, T. S., J. F. Valentine, and L. B. Lutz.
1987. An illustrated guide with key to selected benthic invertebrate fauna of the northern Gulf of Mexico, 163 p. Mississippi-Alabama Sea Grant Consortium MAS-GP-87-0100. Dauphin Island Sea Laboratory, Dauphin Island, AL. [Available at website.]

Humphries, A. T., M. K. La Peyre, and G. A. Decossas.
2011a. The effect of structural complexity, prey density, and "predator-free space" on prey survivorship at created oyster reef mesocosms. PLoS ONE. 6(12): e28339.

Humphries, A. T., M. K. La Peyre, M. E. Kimball, and L. P. Rozas.
2011b. Testing the effect of habitat structure and complexity on nekton assemblages using experimental oyster reefs. J. Exp. Mar. Biol. Ecol. 409:172–179.

Jacob, U., K. Mintenbeck, T. Brey, R. Knust, and K. Beyer.
2005. Stable isotope food web studies: a case for standardized sample treatment. Mar. Ecol. Prog. Ser. 287:251–253.

Jones, C. G., J. H. Lawton, and M. Shachak.
1994. Organisms as ecosystem engineers. Oikos 69: 373–386. [Available at website.]
1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Kells, V., and K. Carpenter.
2011. A field guide to coastal fishes from Maine to Texas, 448 p. The Johns Hopkins Univ. Press, Baltimore, MD.

Kirby, M. X.
2004. Fishing down the coast: historical expansion and collapse of oyster fisheries along continental margins. Proc. Natl. Acad. Sci. 101:13096–13099.

La Peyre, M. K., J. Furlong, L. A. Brown, B. P. Piazza, and K. Brown.
2014b. Oyster reef restoration in the northern Gulf of Mexico: extent, methods and outcomes. Ocean Coast. Manage.89:20–28.

La Peyre, M. K., A. T. Humphries, S. M. Casas, and J. F. La Peyre.
2014a. Temporal variation in development of ecosystem services from oyster reef restoration. Ecol. Eng. 63: 34–44.

Layman, C. A., D. A. Arrington, C. G. Montaña, and D. M. Post.
2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48.

Lehnert, R. L., and D. M. Allen.
2002. Nekton use of subtidal oyster shell habitat in a southeastern U.S. estuary. Estuaries 25:1015–1024.

Lenihan, H. S.
1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. Ecol. Monogr. 69:251–276.

Lenihan, H. S., and F. Micheli
2000. Biological effects of shellfish harvesting on oyster reefs: resolving a fishery conflict by ecological experimentation. Fish. Bull. 98:86–95.

Lenihan, H. S., and C. H. Peterson.
1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. Ecol. Appl. 8:128–140.
2004. Conserving oyster reef habitat by switching from dredging and tonging to diver-harvesting. Fish. Bull. 102:298–305.

Lenihan, H.S., C. H. Peterson, J. E. Byers, J. H. Grabowski, G. W. Thayer, and D. R. Colby.
2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. Ecol. Appl. 11:764–782.

Lonsdale, D. J., R. M. Cerrato, R. Holland, A. Mass, L. Holt, R. A. Schaffner, J. Pan, and D. A. Caron.
2009. Influence of suspension-feeding bivalves on the pelagic food webs of shallow, coastal embayments. Aquat. Biol. 6:263–279.

MacIntyre, H. L., and J. J. Cullen.
1996. Primary production by suspended and benthic microalgae in a turbid estuary: time scales of variability in San Antonio Bay, Texas. Mar. Ecol. Prog. Ser. 145:245–268.

Newell, R. I. E., T. R. Fisher, R. R. Holyoke, and J. C. Cornwell.
2005. Influence of eastern oysters on nitrogen and phosphorus regeneration in Chesapeake Bay, USA. *In* The comparative roles of suspension feeders in ecosystems. NATO Sci. Ser.: IV Earth Enviorn. Sci., vol. 47 (R Dame and S. Olenin eds.), p. 93–120. Springer, Netherlands.

Officer, C. B., T. J. Smayda, and R. Mann.
1982. Benthic filter feeding - a natural eutrophication control. Mar. Ecol. Prog. Ser. 9:203–210.

Peterson, C. H., J. H. Grabowski, and S. P. Powers.
2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Mar. Ecol. Prog. Ser. 264:249–264.

Piehler, M. F., and A. R. Smyth.
2011. Habitat-specific distinctions in estuarine denitrification affect both ecosystem function and services. Ecosphere 2:article 12.

Post, D. M.
2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Quan, W., A. T. Humphries, L. Shi, and Y. Chen.
2012. Determination of trophic transfer at a created intertidal oyster (*Crassotrea ariakensis*) reef in the Yangtze River Estuary using stable isotope analyses. Estuar. Coasts 35:109–120.

Rice, E. W., R. B. Baird, A. D. Eaton, and L. S. Clesceri (eds.).
2012. Standard methods for the examination of water and wastewater, 22nd ed., 1496 p. American Public Health Association, Washington, D.C.

Rothschild, B. J., J. S. Ault, P. Goulletquer, and M. Héral.
1994. Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. Mar. Ecol. Prog. Ser. 111:29–39.

Soniat, T. M., C. M. Finelli, and J. T. Ruiz.
2004. Vertical structure and predator refuge mediate oyster reef development and community dynamics. J. Exp. Mar. Biol. Ecol. 310:163–182.

Summerhayes, S. A., M. J. Bishop, A. Leigh, and B. P. Kelaher.
2009. Effects of oyster death and shell disarticulation on associated communities of epibiota. J. Exp. Mar. Biol. Ecol. 379:60–67.

ter Braak, C. J. F., and P. Smilauer.
2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (vers. 4.5), 500 p. MicrocomputerPower, Ithaca, NY.

Thompson, B. A.
1986. Identification guide to selected estuarine fishes of Louisiana. Louisiana Sea Grant College Program and Louisiana State Univ. Coastal Fisheries Institute LSU-CFI-86-05, 29 p. Center for Wetlands Resources, Louisiana State Univ., Baton Rouge, LA. [Available at website.]

Tolley, S. G., and A. K. Volety.
2005. The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. J. Shellfish Res. 24:1007–1012.

Vanderklift, M. A., and S. Ponsard.
2003. Sources of variation in consumer-diet ^{15}N enrichment: a meta-analysis. Oecologia 136:169–182.

Yeager, L. A., and C. A. Layman.
2011. Energy flow to two abundant consumers in a subtropical oyster reef food web. Aquat. Ecol. 45:267–277.

zu Ermgassen, P. S. E., M. D. Spalding, R. E. Grizzle, and R. D. Brumbaugh.
2013. Quantifying the loss of a marine ecosystem service: filtration by the eastern oyster in US estuaries. Estuar. Coasts 36:36–43.

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Inferred historical fishing mortality rates for an endangered population of Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract—The time series of estimated fishery exploitation rates for endangered Sacramento River winter Chinook salmon (*Oncorhynchus tshawytscha*) is confined to a relatively recent period for which coded-wire tag data have been available. However, the nature of ocean salmon fisheries before this period was substantially different, and it is likely that recent exploitation rates do not represent the level of fishing mortality experienced by these Chinook salmon in earlier years. To infer historical exploitation rates, a model was developed to hindcast the impact rate for age-3 winter Chinook salmon (an approximation of the exploitation rate) by using 35 years of fishing effort estimates coupled with contemporary estimates of fishery encounter rates. The impact-rate hindcasts were highest during a period from the mid-1980s through the mid-1990s. Over time, the proportion of the impact rate attributed to commercial and recreational fisheries diverged from approximately equal shares early in the time series to an impact rate mostly composed of recreational fishery-induced mortality in more recent years. The inferred exploitation rates provide context for the fishing-induced mortality experienced by winter Chinook salmon both before and after the time of the initial inclusion of this species on the Endangered Species Act (ESA) list in 1989 and through a dynamic period for ocean salmon fisheries in California.

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Determining the status of a stock often entails estimation of the population state or exploitation rate in relation to a baseline period before, or in the early stages of, a developing fishery. For example, determinations of an overfished status for many fish populations rely on estimates of depletion: the spawning stock biomass expressed as a fraction of its unfished level (Restrepo and Powers, 1999; Haltuch et al., 2008). The determination of Endangered Species Act (ESA) status for Pacific salmon (*Oncorhynchus* spp.) populations include analysis of current abundance levels in relation to the habitat carrying capacity and historical population abundance (Myers et al., 1998). The effect of fisheries (e.g., overfishing) generally is inferred from a time series of exploitation rate estimates that are compared with benchmarks of sustainable or optimal fishing-induced mortality rates. Estimation of historical fishing mortality rates is a focus of stock assessment, and such estimates are necessary inputs into life cycle models that allow inferences to be drawn regarding population dynamics in the face of competing sources of mortality (Hendrix et al., 2014). Because there are often only short data series available for many stocks of conservation concern to allow evaluation of their status, development of approaches that can extend estimated abundance or exploitation rates retrospectively can improve our historical understanding of a stock's dynamics.

For Pacific salmon, the time series of estimated exploitation rates can often be quite short because stock-specific catch data must be garnered from mixed-stock ocean fisheries, where the stock of origin cannot be determined visually, and therefore the estimate of exploitation rates requires tagging data (most commonly with a coded-wire tag; Johnson, 1990; Lapi et al., 1990; Nandor et al., 2010) or potentially genetic data (Milner et al., 1985; PSC[1]; Satterthwaite et al., 2014). Estimates of exploitation rates are frequently confined to a period of time after major changes in the fishing capacity of fleets, allowing for only a glimpse of

[1] PSC (Pacific Salmon Commission). 2008. Recommendations for application of genetic stock identification (GSI) methods to management of ocean salmon fisheries. Special report of the GSI steering committee and the Pacific Salmon Commission's committee on scientific cooperation. Pacific Salmon Comm. Tech. Rep. 23, 35 p. [Available at website.]

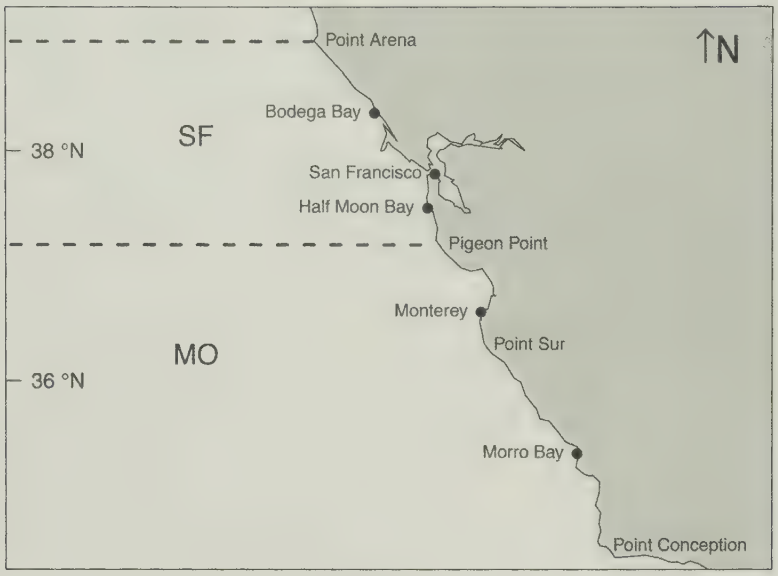

Figure 1

Map of the central California coastline, with the northern boundaries of the San Francisco (SF) and Monterey (MO) management areas denoted by dashed lines.

how exploitation has varied historically. This general condition applies to both target stocks in fisheries, as well as ESA-listed stocks that are taken in fisheries as incidental catch.

Sacramento River winter Chinook salmon (*Oncorhynchus tshawytscha*) (SRWC), named for the season of freshwater spawning return, were first listed under the ESA in 1989 as threatened and then as endangered in 1994 (Federal Register, 1994). The Sacramento River winter Chinook Evolutionarily Significant Unit, currently composed of a single population that spawns in the Sacramento River downstream from Keswick and Shasta dams near Redding, California, has experienced a heavy decline in abundance (Fisher, 1994; Yoshiyama et al., 1998). Fisher (1994) reported a potential maximum spawning run size of 200,000 before dam construction and a spawning stock estimate of more than 100,000 fish in the late 1960s (after dam construction). Estimates published by the Pacific Fishery Management Council (PFMC) (PFMC[2]) indicate a run size of more than 30,000 fish in the early 1970s and run sizes below 1000 fish for several years since 1980.

The time series of exploitation rates estimated for SRWC is much shorter than the time series for escapement. O'Farrell et al. (2012a) used cohort reconstruction methods (Hilborn and Walters, 1992) to estimate broad year exploitation rates, referred to as the *spawner reduction rate* and defined as the reduction in a brood's potential adult spawner escapement that is caused by ocean fisheries in relation to escapement potential in the absence of ocean fishing. A cohort-reconstruction model was applied to data generated from the SRWC marking (with adipose fin clips) and tagging (with coded-wire tags) program initiated at Livingston Stone National Fish Hatchery in 1998. Before 1998, hatchery supplementation of SRWC was sporadic and the marking and tagging data were insufficient for estimation of exploitation rates. The impact rate for age-3 SRWC (hereafter referred to as the *impact rate*) is a measure of the fishing mortality rate on age-3 fish that corresponds closely to the exploitation rate for SRWC. The correspondence between the brood-year exploitation rate and the impact rate is due to the very high maturation rates of age-3 SRWC that result in few age-4 fish remaining in the ocean to contribute to catch or spawner escapement (O'Farrell et al., 2012a). The impact rate is estimated annually and published in PFMC reports (e.g., PFMC[3]).

Although the estimated impact rates quantify the recent (during and after the year 2000) salmon fishing-induced mortality (hereafter "fishery mortality") on SRWC, this period follows the implementation of conservation measures designed to reduce impacts on SRWC and changes in ocean fisheries owing to management measures intended for other stocks. Salmon fisheries south of Point Arena, California (Fig. 1), are responsible for the vast majority of SRWC harvest (O'Farrell et al., 2012a; Satterthwaite et al., 2013), and many of the constraints on fisheries in this region have been intended to protect SRWC. For example, recreational fisheries in this region routinely began in mid-February, but since the early 1990s the starting date gradually moved later in the year. Since 2004, no fisheries have occurred in February or March. Increased minimum size limits (e.g., >20 in [51 cm] in total length) have been imposed on the recreational sector in an effort to reduce retention of SRWC. For a variety of reasons associated with increased constraints on ocean fishing that have resulted from ESA listings and river (versus-ocean) allocations of harvest, the commercial sector has seen a reduction in participation of vessels with California salmon permits since the early 1980s (PFMC[2]). The time series of commercial and recreational fishing effort south of Point Arena (Fig. 2) indicates that substantial changes in ocean fishery ef-

[2] PFMC (Pacific Fishery Management Council). 2014. Review of 2013 ocean salmon fisheries: stock assessment and fishery evaluation document for the Pacific coast salmon fishery management plan, 371 p. (Document prepared for the Council and its advisory entities.) Pacific Fishery Management Council, Portland, OR [Available at website.]

[3] PFMC (Pacific Fishery Management Council). 2015. Preseason report I: stock abundance analysis and environmental assessment part 1 for 2015 ocean salmon fishery regulations, 135 p. (Document prepared for the Council and its advisory entities.) Pacific Fishery Management Council, Portland, OR. [Available at website.]

fort have occurred since the late 1970s and the inferred fishing effects for recent SRWC cohorts may not be indicative of earlier exploitation patterns.

In this article, we describe a model for the hindcasting of fishery impact rates to assess the implications for SRWC fishing mortality resulting from changes in California salmon fisheries that have occurred over the past 35 years. The model uses data on historical fishery regulations and estimates of fishing effort in California salmon fisheries in 1978–2012, and it couples these estimates with contact (i.e., fishery encounter) rates per unit of fishing effort estimated for recent years (2000–2012), to generate hindcasts of the impact rate for years when direct estimation is not possible. To fully parameterize the model, we developed a procedure to infer contact rates per unit of effort for months when no direct estimates exist because of the contraction of modern fisheries in relation to fisheries from the 1970s through the 1990s. The model structure is similar to the Winter Run Harvest Model (WRHM; O'Farrell et al., 2012b), a tool used to forecast the impact rate during the annual PFMC salmon fishery planning process. Although we are not able to reconstruct the complete SRWC exploitation history, the extension of the impact rate time series back to 1978 encompasses a dynamic period for California ocean salmon fisheries and provides more context for the current levels of ocean fishing mortality.

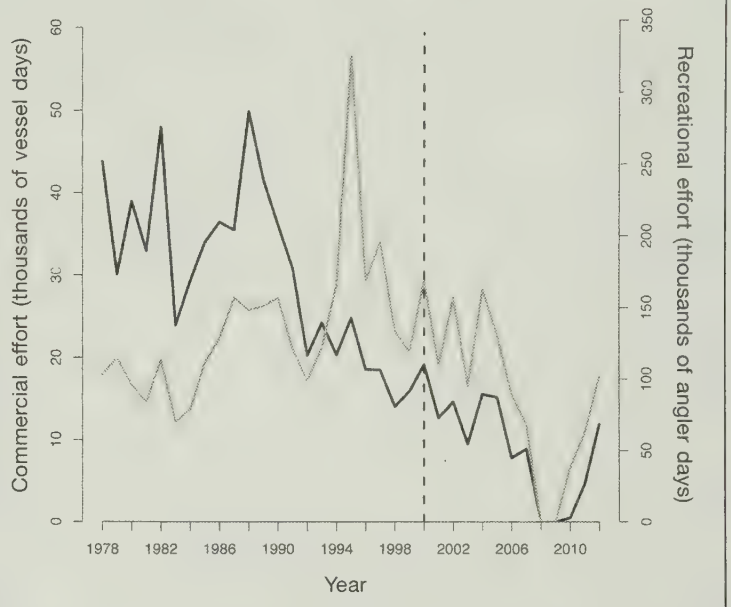

Figure 2

Estimates of commercial (black line) and recreational (gray line) sector fishing effort for the years 1978–2012 in ocean areas south of Point Arena, California. Direct estimates of the Sacramento River winter Chinook salmon (*Oncorhynchus tshawytscha*) impact rate have been made with cohort reconstruction methods for the years to the right of the dashed line (post-2000). Note that fishing effort units differ between the commercial and recreational fisheries and are not directly comparable.

Materials and methods

Impact-rate model

The data and model used for this analysis were stratified by year (y), month (t), management area (z), and fishery sector (x). Because harvest of SRWC is rare north of Point Arena, California (O'Farrell et al., 2012a; Satterthwaite et al. 2013), the spatial extent of our model is limited to the 2 ocean management areas south of Point Arena: San Francisco (SF) and Monterey (MO) (Fig. 1). The MO management area extends from Pigeon Point to the border of the United States and Mexico, but salmon harvest is generally small and more variable south of Point Sur. Fishery sectors include commercial and recreational.

Fishery impacts (I) included fish that died because they were retained as harvest (H), fish that were released because they were smaller than the minimum size limit and died because of release mortality (S), and fish that died from "dropoff" mortality (D) that occurs when fish are encountered by fishing gear but not successfully retrieved. Mortality related to an encounter with gear can come from multiple sources, such as a hooking injury or predators (PFMC[4], and the references therein). The impact rate is defined as the total fishing mortality, acute and delayed, divided by the starting cohort abundance.

The impact-rate model simulates the age-3 cohort abundance from the beginning of age 3, t=February of year (y), to t=January of year y+1,

$$N_{t+1} = (N_t - I_t)(1 - v). \quad (1)$$

by deducting monthly impacts, $I_t = \Sigma_{z,x} I_{t,z,x}$, and accounting for the natural mortality rate v. Application of Equation 1 over months t enables the computation of the annual impact rate, defined as the sum of monthly impacts divided by the initial abundance of age-3 fish:

$$i = \frac{\Sigma_t I_t}{N_{t=\text{February}}}. \quad (2)$$

Impacts are computed from a string of equations initiated by an estimate of the contact rate c, which is formulated as the contact rate per unit of effort β, multiplied by the amount of fishing effort f,

[4] PFMC (Pacific Fishery Management Council). 2000. STT recommendations for hooking mortality rates in 2000 recreational ocean Chinook and coho fisheries. STT Rep. B.2, 18 p. Pacific Fishery Management Council, Portland, OR. [Available at website.]

$$c_{t,z,x} = \beta_{t,z,x} \times f_{t,z,x}. \quad (3)$$

The number of fish contacted (C) is computed by multiplying the oceanwide abundance of the SRWC age-3 cohort by the contact rate:

$$C_{t,z,x} = c_{t,z,x} \times N_t, \quad (4)$$

where contacts represent the number of fish that encountered the fishing gear and were retrieved to the boat. Impacts are the sum of harvest, release, and dropoff mortality:

$$I_{t,z,x} = H_{t,z,x} + S_{t,z,x} + D_{t,z,x} \quad (5)$$

where

$$H_{t,z,x} = C_{t,z,x} \times p_{t,z,x}, \quad (6)$$

$$S_{t,z,x} = (C_{t,z,x} - H_{t,z,x}) \times s_{t,z,x}, \quad (7)$$

and

$$D_{t,z,x} = C_{t,z,x} \times d. \quad (8)$$

In these equations, release and dropoff mortality rates are denoted by s and d, respectively, and p is the estimated proportion of the cohort that is greater than or equal to the legal size for retention in the fishery.

Data, parameters, and variables

Effort in California ocean salmon fisheries was estimated by the California Department of Fish and Wildlife (CDFW) on the basis of landing receipts from the commercial sector and dockside samples from the recreational sector. Units of fishing effort are the number of vessel days (the number of days fished by commercial salmon vessels) for the commercial sector and number of angler days for the recreational sector. Fishing effort for the years 1978–2012 are reported in PFMC[2] and an electronic record of the historical ocean salmon fishery effort and landings for the U.S. West Coast (PFMC[5]), maintained by the PFMC. Records of minimum size limits in California ocean fisheries for the years 1978–2012 were obtained from PFMC[2] and an electronic record of the historical ocean salmon fishery regulations for the U.S. West Coast (PFMC[6]), maintained by the PFMC.

Coded-wire tag recovery data from ocean and river sampling programs were used in cohort reconstructions for SRWC to estimate contact and impact rates in ocean fisheries for the years 2000–2012, following the methods described in O'Farrell et al. (2012a). Cohort reconstruction is the sequential estimation of a cohort's abundance from the end of that cohort's life span, when abundance is zero, to a specified earlier age (commonly age 2). Age-specific spawner escapement and harvest data are required, and natural mortality rates are assumed. Fishery contacts stratified by age, month, management area, and fishing sector were computed by expanding the harvest by the estimated proportion of SRWC expected to be larger than or equal to the minimum size limit ($C = H/p$). Given an estimate of C, and the estimated abundance N, the contact rate was estimated by rearranging Equation 4 as follows: $c = C/N$. The impact rate was estimated from cohort reconstruction in the same manner as that shown in Equation 2.

It was implicitly assumed that contact and impact rates estimated from tagged, hatchery-origin fish are representative of the natural-origin SRWC population. Although it is difficult to directly evaluate this common assumption (PSC[7]), there is some evidence that hatchery-origin indicator stocks have similar ocean distributions and fishery exposure as those estimated for untagged stocks for which they serve as proxies (Weitkamp and Neely, 2002; Satterthwaite et al., 2014). The hatchery-origin component of the total SRWC abundance is only a portion of the total abundance; for the years 2000–2010, the hatchery-origin component of female SRWC spawners was ≤20% (Winship et al., 2014). Ocean salmon fisheries are sampled by the CDFW with a goal of sampling at least 20% of the harvest in each month, management area, and fishery sector. Heads are taken from all fish with a clipped adipose fin for coded-wire tag extraction and reading. A total of 4036 coded-wire tag recoveries were used in cohort reconstructions, 554 of which were from ocean fisheries (commercial and recreational), whereas the vast majority of the remaining recoveries were from spawner escapement surveys. Recreational, river harvest of SRWC is rare because of closures to the Sacramento River salmon fishery during much of the migration and spawning period.

Contact rates and fishing effort estimated for each month, area, and sector open to fishing in 2000–2012 were used to calculate the contact rate per unit of effort. For hindcasting purposes, values of the contact rate per unit of effort were derived for the entire period of 1978 to 2012 with the application of the bootstrap method to the estimates of contact rates per unit of effort for 2000–2012 (Efron and Tibshirani, 1993). These derived values of contact rate per unit of effort were then multiplied by the corresponding observed fishing effort for 1978–2012 to yield a set of contact rate hindcasts (Eq. 3). The bootstrap method used to characterize the contact rates per unit of effort is described later in the "Bootstrap" subsection. For strata for which these rates could not be estimated from available data sources, 2 methods were used to infer contact rates per unit of effort.

Data sufficient for estimation of contact rates per unit of effort for recreational fisheries during February and March are not available because recreational

[5] PFMC (Pacific Fishery Management Council). 2014. Ocean salmon fishery effort and landings (Review Appendix A). Excel workbook. PFMC, Portland, OR. [Available at website.]

[6] PFMC (Pacific Fishery Management Council). 2014. Ocean salmon fishery regulations and chronology of events (Review Appendix C). PFMC, Portland, OR. [Available at website.]

[7] PSC (Pacific Salmon Commission). 2005. Report of the expert panel on the future of the coded wire tag program for Pacific salmon. Pacific Salmon Comm. Tech. Rep. 18, 230 p. [Available at website.]

fisheries in the 2000–2012 period were largely closed during these months. To infer contact rates per unit of effort for these strata, we used historical SRWC harvest data derived from marked (fin-clipped) natural-origin fish from the brood years 1969–1970 that were recovered in ocean fisheries as age-3 fish during the calendar years 1971–1972 (CDFG[8]). Recreational fisheries in SF and MO in 1971–1972 opened in mid-February with a 22-in (56-cm) minimum size limit, and this timing of the start of the season and this minimum size restriction were similar for recreational fishing seasons through 1983. The average proportion of the recreational harvest of age-3 SRWC south of Point Arena that was taken in February–March for the years 1971–1972 (ϕ_1) was 0.33. This proportion was assumed to be representative of the average fraction of the recreational harvest south of Point Arena that was taken in February and March for the years 1978–1983 (ϕ_2). Assuming that the contact rate per unit of effort was equivalent for February and March, and in management areas SF and MO, we used the root finding function uniroot in the R statistical software, vers. 3.0.0 (R Core Team, 2013) to identify the value of contact rate per unit of effort that resulted in the difference between ϕ_1 and ϕ_2 that equaled zero. Put another way, we solved iteratively for the contact rates per unit of effort for February–March that resulted in 33% of the total recreational sector harvest occurring in February–March, on average, for the years 1978–1983.

Data sufficient for estimation of contact rates per unit of effort also do not exist for the commercial sector in SF or MO in April and for the recreational sector in MO in October because fisheries in the 2000–2012 period were largely closed for these months. In the case when SF and MO commercial fisheries began in April, the estimate of contact rate per unit of effort for May was assumed. In the case when MO recreational fisheries extended into October, the contact rate per unit of effort for September was assumed. These assumptions had little effect on the results because April commercial fisheries and MO recreational fisheries in October were relatively rare, were short in duration, and attracted little effort.

The proportion of SRWC expected to be of legal size for retention was determined on the basis of a size-at-age model derived for SRWC, described in O'Farrell et al. (2012a, 2012b), and the specified minimum size limit for retention in a fishery. For the growth model, the size-at-age of individual fish in each month is assumed to be normally distributed, and the proportion of legal-size fish is estimated by evaluating the cumulative normal distribution at the minimum size limit, given the estimated mean and standard deviation. When a large minimum size limit is in effect for months when SRWC size-at-age is smallest (i.e., February–May), very low estimates of the proportion of legal-size fish can result. This scenario can translate into unrealistically low levels of harvest per contacted fish, and, conversely, into a very large estimate of contacts based on a single retained and sampled fish. As a result, a lower bound on the proportion of legal-size fish of 0.035 is assumed. The value of 0.035 corresponds to the condition where a single coded-wire tag recovery results in contacts approximately equivalent to the lowest reconstructed abundance of age-3 fish estimated from cohort reconstruction (O'Farrell et al., 2012a). Use of this lower bound value reduces the probability that an entire hatchery-origin cohort would be estimated to be contacted by the fishery in order to produce one harvested and sampled fish. Table 1 displays the size-at-age model parameters and the proportion of legal-size fish estimated for commonly employed minimum size limits in both the commercial and recreational fisheries.

Release mortality rates were assumed to be 0.26 for the commercial sector and 0.14 for the recreational sector, reflecting the conventional values used for the annual assessment of SRWC and other Chinook salmon stocks (PFMC[4]). An exception exists in the recreational sector, where release mortality rates for 1990–2012 were estimated on the basis of prevalence of *mooching* (drifting a hooked bait in the California recreational sector), and fish contacted with mooching gear experience a higher rate of gut hooking and, therefore, a higher release mortality rate than that of troll-contacted fish (Grover et al., 2002). Derived from the results in Grover et al. (2002), estimates of the recreational release mortality rate range from 0.14 to 0.57 between 1990 and 2012 (Grover[9]).

The dropoff mortality rate was assumed to be 0.05 for all months, areas, and sectors, reflecting the conventional value used for PFMC Chinook salmon assessment (PFMC[4]).

The natural mortality rate was assumed to be 0.018, the monthly rate corresponding to an annual natural mortality rate of 0.20. The annual natural mortality rate of 0.20 is commonly assumed in many stock assessments (Quinn and Deriso, 1999) and is consistent with many PFMC Chinook salmon assessments (e.g., O'Farrell et al., 2012a, 2012b).

Bootstrap

A key source of uncertainty in the hindcasting of impact rates is variation in estimates of contact rates per unit of effort across years. To account for this variation, we performed 20,000 replicate computations of the impact rate for the years 1978–2012 by randomly sampling, with replacement, estimates of the contact rate per unit of effort from the years 2000–2012. This procedure effectively makes the assumption that annual variation in contact rate per unit of effort in 2000–2012 is representative of the entire time series for 1978–2012. For

[8] CDFG (Calif. Dep. Fish Game). 1989. Unpubl. report. Description of the winter Chinook Ocean Harvest Model. Ocean Salmon Project, Calif. Dep. Fish Game, Santa Rosa, CA.

[9] Grover, A. 2013. Personal commun. Institute of Marine Sciences, Univ. Calif., Santa Cruz, Santa Cruz, CA 95064.

Table 1

Estimates of the mean (μ) and standard deviation (σ) of the size-at-age distribution, by month, and the resulting proportion of legal-size fish (p) under three commonly employed minimum size limits (l). Size units are total length in inches.

				p		
Year	Month	μ	σ	l=20	l=24	l=26
y	Feb	19.74	1.66	0.438	0.035	0.035
	Mar	20.77	1.70	0.674	0.035	0.035
	Apr	21.85	1.79	0.849	0.115	0.035
	May	22.94	1.88	0.941	0.286	0.052
	Jun	24.02	1.97	0.979	0.504	0.157
	Jul	25.10	2.06	0.993	0.704	0.331
	Aug	26.20	2.15	0.998	0.847	0.537
	Sep	27.28	2.24	0.999	0.929	0.717
	Oct	28.37	2.33	1.000	0.970	0.846
	Nov	29.45	2.41	1.000	0.988	0.923
	Dec	29.72	2.44	1.000	0.991	0.937
y+1	Jan	29.21	2.40	1.000	0.985	0.910

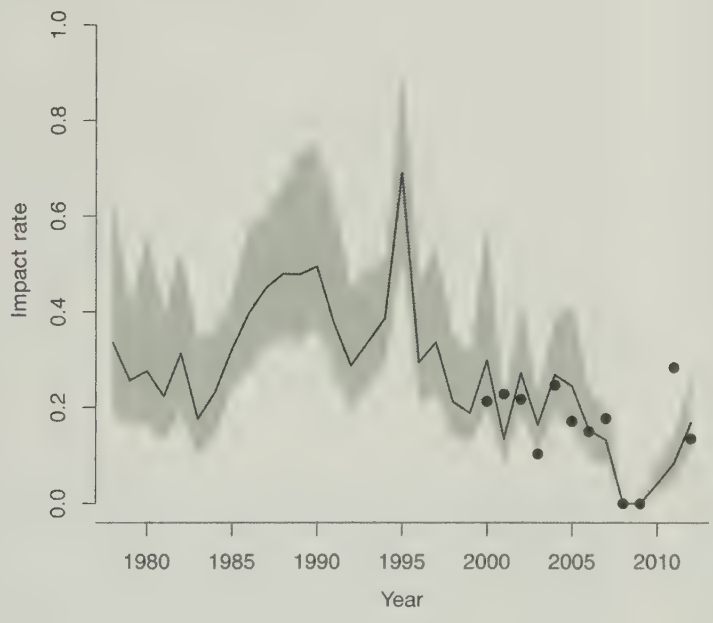

Figure 3

Time series of hindcast impact rates for the years 1978–2012 for Sacramento River winter Chinook salmon (*Oncorhynchus tshawytscha*) south of Point Arena, California. The black line represents the median, and the shaded area indicates the 0.68 percentile interval of the bootstrap distribution. The dots indicate estimates of the impact rate derived with cohort reconstruction methods.

each replication, an estimate of contact rate per unit of effort was sampled independently for each month, management area, and sector in the period 2000–2012 and applied to the years 1978–2012. For the inferred contact rate per unit of effort in February and March for the recreational fishery, the root-finding procedure was performed as previously described in each of the 20,000 replications. Impact-rate uncertainty was characterized by the 0.68 percentile interval of the 20,000 replication bootstrap distribution (Efron and Tibshirani, 1993). For a normally distributed estimator, the 0.68 percentile interval corresponds to the mean ± 1 standard error (Zar, 1999).

Results

Model results provide evidence that the highest impact rates occurred between the mid-1980s and the mid-1990s followed by a substantial decrease (Fig. 3). For several years in the period 1985–1995, the lower bound of the 0.68 percentile interval exceeded the upper bound of the 0.68 percentile interval for the post-2000 period. The hindcasts from the impact-rate model generally captured the variation in the impact rates estimated directly from coded-wire tag data by using cohort reconstruction methods in recent years.

There was evidence for a substantial difference in the impact-rate trajectories between the commercial and recreational sectors (Fig. 4A). The impact-rate time series for the commercial sector showed a nearly monotonic decline from 1978 through 2012. In contrast, the impact rate for the recreational sector exhibited much more variation, and maximum impact rates occurred in the middle of the time series. This pattern of sector-specific impact rates led to divergence in the proportions of the impact rate attributable to the 2 sectors over time (Fig. 4B). In the early portion of the time series (before the mid-1980s), the commercial and recreational sectors contributed approximately equally to the total impact rate. Subsequently, the share of the impact rate attributed to the recreational sector increased and stabilized at approximately 80% of the overall impact rate.

Estimates of contact rates per unit of effort that were used to inform the impact-rate hindcasts differed across fishery sectors and management areas (Fig. 5). Distributions of month-specific contact rates per unit of effort in most cases were skewed, with the mean exceeding the median. This pattern was most evident in the MO management area where the maximum contact rates per unit of effort in both the commercial and recreational sectors were much higher than the corresponding sectors in the SF manage-

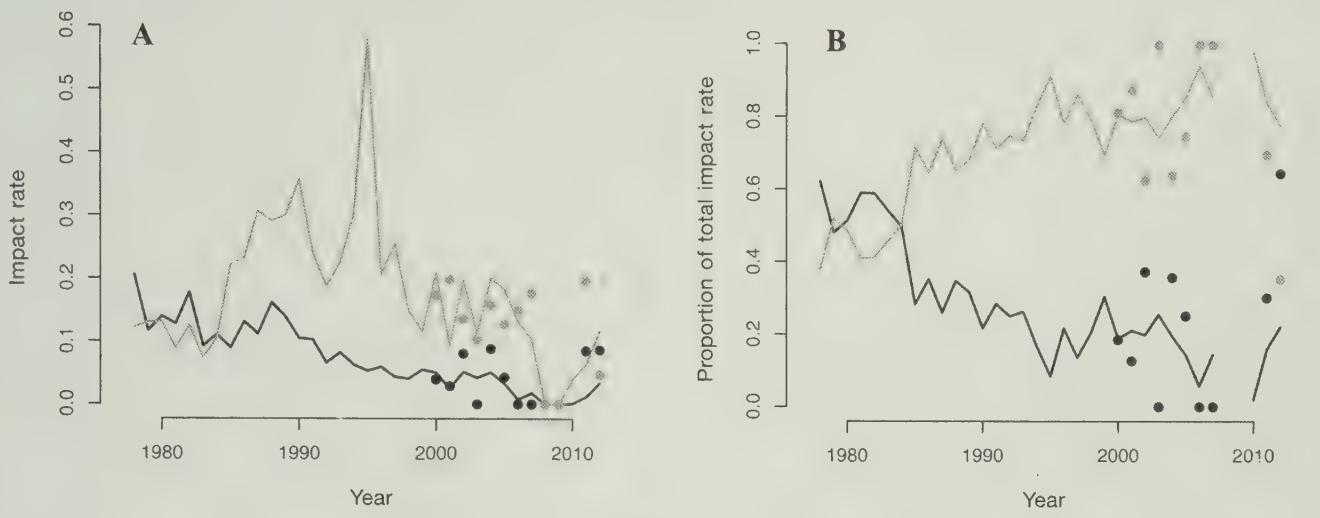

Figure 4

Estimates of the median (**A**) impact rates and (**B**) impact rate proportions for Sacramento River winter Chinook salmon (*Oncorhynchus tshawytscha*) south of Point Arena, California, for the commercial (black lines) and recreational (gray lines) sectors. The dots indicate estimates of the impact rates derived with cohort reconstruction methods.

ment area, and, therefore, there were larger differences between the median and mean estimates of the contact rate per unit of effort in MO in relation to SF. In many cases, the median contact rates per unit of effort were zero, particularly in the commercial sector. For recreational fisheries in February and March, inferred contact rates per unit of effort were much higher than estimates for other months. These values were higher than all estimates of contact rates per unit of effort in the SF management area and were among the highest values observed in the MO area. These high contact rates per unit of effort were not unexpected given the high proportion of the total harvest that occurred in February and March, according to estimates derived from the data for 1971–1972 (ϕ_1=0.33), and given the low estimates of the proportion of legal-size fish for these months (Table 1). High levels of contact rates per unit of effort in February and March would be required to result in the substantial harvest proportions in those months and, therefore, to approximate the monthly harvest distributions from the data for 1971–1972.

To evaluate whether the impact-rate hindcasts had a pattern similar to measures of fishing mortality for other stocks subjected to a common ocean fishery, we compared the median SRWC impact-rate hindcasts with Sacramento River fall Chinook salmon (SRFC) harvest rates directly estimated from coded-wire tag data. The SRFC stock is the largest contributor to ocean salmon fisheries south of Point Arena. Harvest rates were estimated by computing the ratio of SRFC adult (ages 3–5) harvest south of Point Arena to the Sacramento Index (the Sacramento Index is the sum of ocean harvest south of Cape Falcon, Oregon; river harvest; and spawner escapement; see O'Farrell et al., 2013, for a detailed description). The impact-rate hindcasts for SRWC were highly correlated to SRFC harvest rates in 1983–2012, the years for which the SRFC harvest rate is estimable (correlation coefficient [r]=0.827, P<0.001) (Fig. 6).

Discussion

The large changes in California ocean salmon fisheries over the past 35 years have resulted in substantial changes to the levels of fishing mortality experienced by SRWC. Impact-rate hindcasts indicate lower rates in the 2000s than those in the mid-1980s through the mid-1990s. A decline in the impact rate was evident for the recreational sector following a peak in the 1980s and 1990s, and a decline has been observed for the commercial sector throughout the entire period. The trajectories of the sector-specific impact rates (Fig. 5A) reflect the observed changes in fishing effort (Fig. 2). The strong correlation between harvest rates for SRFC in the region south of Point Arena and the impact-rate hindcasts for SRWC, where both populations have been subjected to the same fisheries, supports the hindcasting methods for calculating impact rates used in this study.

In their analysis of the brood years 1998–2007, O'Farrell et al. (2012a) reported that exploitation rates experienced by SRWC averaged approximately 20% and that the bulk of the ocean impacts were the result of the recreational sector. Although the results from our study are consistent with O'Farrell et al. (2012a) over the common time period, they indicate that recent estimates of the impact rate are unlikely to represent the

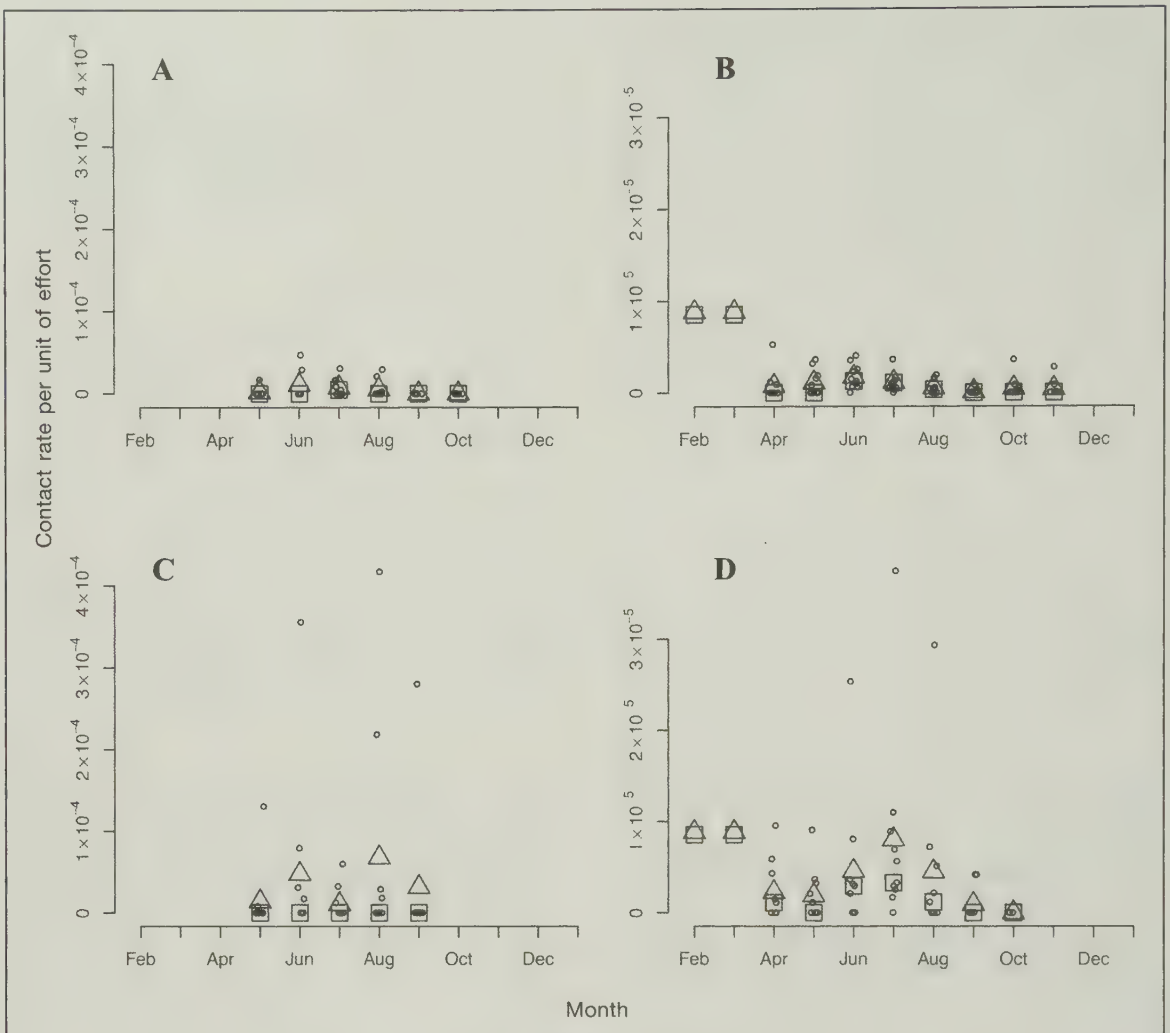

Figure 5

Sacramento River winter Chinook salmon (*Oncorhynchus tshawytscha*) contact rates per unit of effort for the (A) commercial and (B) recreational sectors in the San Francisco (SF) management area and for the (C) commercial and (D) recreational sectors in the Monterey (MO) management area. Circles denote estimated values for individual years, triangles indicate mean values, and squares denote median values. The methods used to infer mean and median contact rates per unit of effort for the recreational sector in February and March are described in the text.

degree of fishery exploitation experienced by SRWC in earlier years. These impact-rate hindcasts were used to extend the SRWC stock assessment and have contributed important fishing mortality inputs to a life-cycle model for this population (Hendrix et al., 2014). More generally, an extended time series of fishing mortality rates derived with the methods described here could allow for an extended reconstruction of recruit abundance useful for stock-recruit analysis (PSC[10]).

The impact-rate estimates derived from cohort reconstruction for 2000–2012 reflect many layers of salmon fishery regulations. In particular, ocean fisheries in California frequently have been constrained by conservation concerns and ocean-versus-river fishery allocations for Klamath River fall Chinook salmon (Prager and Mohr, 2001). A collapse of the SRFC stock (Lindley et al., 2009) closed nearly all California ocean salmon fisheries in 2008 and 2009 and heavily constrained fisheries in 2010. The first SRWC-specific constraints to fisheries began after the species was list-

[10]PSC (Pacific Salmon Commission). 1999. Maximum sustained yield or biologically based escapement goals for selected Chinook salmon stocks used by the Pacific Salmon Commission's Chinook Technical Committee for escapement assessment, vol. 1. Pacific Salmon Comm. Joint Chinook Tech. Comm. Rep. TCCHINOOK (99)-3, 104 p. [Available at website.]

ed as threatened under the ESA in 1989. Fishing constraints included establishment of a closed area for the recreational sector near the mouth of San Francisco Bay and implementation of river fishery restrictions (PFMC[11]). Since those initial SRWC conservation measures were implemented, additional SRWC-focused fishery management measures have been established, including truncation of commercial and recreational fishing seasons, increased minimum size limits, and most recently, impact-rate "caps" set annually by a control rule (see Appendix C in PFMC[12]). Although we do not directly link changes in the impact rate to particular management measures, the increased fishery constraints over the past 35 years have clearly influenced the impact rate.

Estimates of contact rates per unit of effort have a strong effect on the impact-rate forecasts made with the Winter Run Harvest Model (O'Farrell et al., 2012b) and, therefore, on the hindcasts presented here. We assumed that contact rates per unit of effort estimated with cohort reconstruction methods for the years 2000–2012 are representative of contact rates per unit of effort in the years before 2000. Contact rates per unit of effort are a function of catchability and stock distribution, and, in the absence of large temporal changes in these components, assuming contemporary contact rates per unit of effort for past years without direct estimates is reasonable. Large changes in catchability in either the commercial or recreational salmon sectors would be unlikely because modes of fishing and associated fishing gear have changed little over the past 35 years. We would also not expect substantial shifts in SRWC ocean distribution over time because this population has been shown to have a relatively compact southerly distribution (O'Farrell et al., 2012a; Satterthwaite et al., 2013).

Nevertheless, there is likely to be nontrivial process and measurement error associated with the estimates of contact rates per unit of effort. Local conditions undoubtedly affect both the ability of fishing fleets to contact SRWC and the precise local concentration of SRWC cohorts. With regard to sampling error, estimates of contact rates per unit of effort are made by using expanded coded-wire tag data and estimates of fishing effort. SRWC coded-wire tag recoveries can be relatively rare for a variety of reasons. SRWC have a lower abundance than that of other Chinook stocks that contribute to California fisheries, and only the hatchery-origin component of the population is marked and tagged. Approximately 20% of the landed catch is sampled, and early-season fisheries with large minimum size limits would be expected to retain few SRWC because few fish would be greater than the minimum legal size.

These sampling issues for rare stocks can readily lead not only to an estimate of zero contacts in a month, area, and sector stratum despite nonzero actual contacts but also to cases where a single tag recovery implies a very large number of contacts. In some strata, estimates of SRWC contact rates have been based on a very small number of coded-wire tag recoveries (O'Farrell et al., 2012a).

To infer values of potential contact rate per unit of effort for the recreational sector in February and March, we developed a method based on estimates of the monthly distribution of harvest when fisheries were open from February through November. The inferred recreational contact rates per unit of effort for February and March from this procedure were higher than estimates of contact rates per unit of effort from months after March, although such high values would be expected given the relatively large proportion of harvest that was estimated for 1971–1972 and the small proportion of age-3 SRWC expected to be greater than the minimum legal size limit during those months.

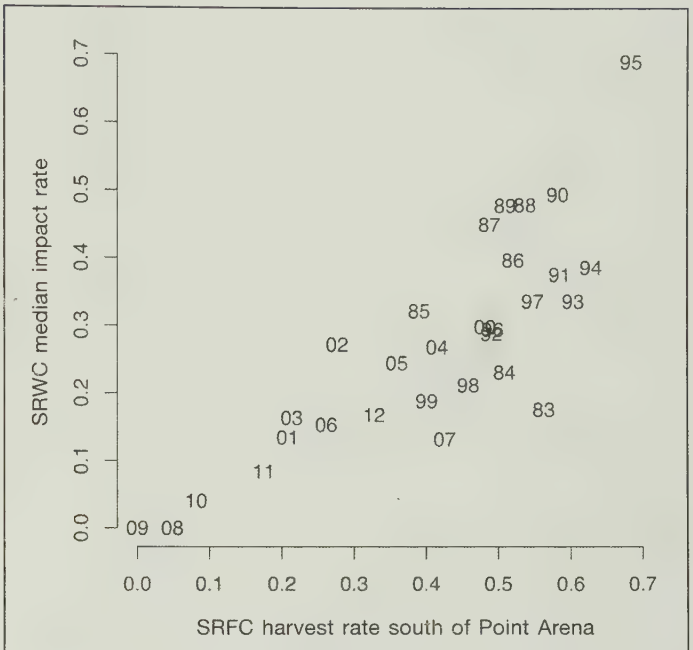

Figure 6

Sacramento River winter Chinook salmon (*Oncorhynchus tshawytscha*) (SRWC) hindcast median impact rates plotted as a function of Sacramento River fall Chinook salmon (SRFC) harvest rates for fisheries south of Point Arena, California. Numbers denote the calendar years 1983–2012.

[11]PFMC (Pacific Fishery Management Council). 1990. Preseason report III: analysis of Council-adopted management measures for 1990 ocean salmon fisheries. Pacific Fishery Management Council, 24 p. Portland, OR. [Available at website.]

[12]PFMC (Pacific Fishery Management Council). 2013. Preseason report I: tock abundance analysis and environmental assessment part 1 for 2013 ocean salmon fishery regulations, 135 p. (Document prepared for the Council and its advisory entities.) Pacific Fishery Management Council, Portland, OR. [Available at website.]

However, these inferences may not adequately describe the pattern of SRWC contacts in these early months.

Given the data available, we were unable to make management-area-specific inferences of recreational contact rates per unit of effort for February and March; yet for later months, the estimated contact rates per unit of effort tended to be considerably higher in MO than in SF. Additionally, estimates of fishing effort for 1971–1972 do not exist; therefore, we assumed that the monthly distribution of effort in those years was similar to the distribution during the years 1978–1983. If substantial differences in effort occurred between these 2 periods, those differences would contribute to errors in the inferred recreational contact rates per unit of effort for February and March. Nonetheless, the monthly harvest estimates for 1971–1972 represent the only information on the temporal patterns of recreational harvest over the protracted seasons that characterized historical fishing.

To account for uncertainty in the hindcasts of impact rates, we incorporated the variation in estimates of contact rates per unit of effort using the bootstrap method. Although this approach did not account for the full spectrum of uncertainty (e.g., natural mortality rate and fishing effort), it is likely that variation in the estimated contact rates per unit of effort represents the dominant uncertainty because of the high level of variability across years and the strong effect that contact rates have on impact-rate projections. Characterizing uncertainty in contact rates per unit of effort by randomly resampling values for month, area, and sector strata, however, may have led to admitting excess uncertainty into the impact-rate hindcasts. For example, in years with extremely high fishing effort (e.g., 1995), a few replications produced unrealistic estimates where fishery impacts exceeded ocean abundance. This outcome was caused by randomly sampling a very high estimate of contact rate per unit of effort that was then multiplied by a very high, stratum-specific effort estimate. This outcome is clearly not tenable and correlations may exist between the contact rate per unit of effort and fishing effort that would prevent extinction by ocean fishing. However, strong evidence of correlations between contact rate per unit of effort and fishing effort were not observed (senior author, unpubl. data), and no covariance structure was incorporated into the simulation framework.

Ultimately, there is a need to understand the effects of all sources of mortality on the dynamics of the endangered SRWC population to better explain its population dynamics. Winship et al. (2014) estimated low overall productivity for SRWC, likely owing to low fecundity and low juvenile survival rates, which resulted in low sustainable fishing mortality rates. In the absence of hatchery supplementation, Winship et al. (2014) estimated a median maximum sustainable level of fishing mortality (analogous to maximum sustainable yield) at an impact rate of 0.17, as well as a rate of 0.25 under recent levels of hatchery supplementation. Regular hatchery supplementation began in 1998 at the SRWC-dedicated Livingston Stone National Fish Hatchery, with little or no hatchery-origin contributions to the population in prior years.

Given the low sustainable impact rates estimated by Winship et al. (2014), and the relatively high median impact rates inferred for the 1980s and 1990s, it is likely that impact rates exceeded maximum sustainable fishing mortality levels and that they could have reached levels identified as unsustainable under conditions with no hatchery supplementation. However, we note that there was substantial uncertainty estimated for both the maximum sustainable impact rates in Winship et al. (2014) and the historical impact rates inferred here. In addition, the results of Winship et al. (2014) were derived with contemporary (post-1998) data, and it is not known whether the estimated productivity, and, therefore, sustainable impact rates, are applicable for earlier time periods.

Although we present a specific case study for SRWC, our ability to hindcast exploitation rates (for years before the existence of sufficient data that would have allowed direct estimation of exploitation rates) should be useful for other fishery applications. The use of forward projection models in a hindcasting mode can help with a better understanding of the relative effects of past fisheries and management actions on fish stocks. Approaches such as the one developed here have the potential to be useful for integrating long-term records with existing stock assessments and for performing retrospective evaluations of the effectiveness of management measures in data-limited situations.

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Literature cited

Efron, B., and R. J. Tibshirani.
1993. An Introduction to the Bootstrap, 436 p. Chapman & Hall, New York.

Federal Register.
1994. Endangered and threatened species; status of Sacramento River Winter-run Chinook salmon; final rule. Federal Register 59:440–450. [Available at website.]

Fisher, F. W.
1994. Past and present status of Central Valley Chinook salmon. Conserv, Biol. 8:870–873.

Grover, A. M., M. S. Mohr, and M. L. Palmer-Zwahlen.
2002. Hook-and-release mortality of Chinook salmon from drift mooching with circle hooks: management implications for California's ocean sport fishery. *In* Catch and release in marine recreational fisheries (J. A. Lucy

and A. L. Studholme, eds.), p. 39–53. Am. Fish. Soc., Bethesda, MD.

Haltuch, M. A., A. E. Punt, and M. W. Dorn.
2008. Evaluating alternative estimators of fishery management reference points. Fish. Res. 94:290–303.

Hendrix, N., A. Criss, E. Danner, C. M. Greene, H. Imaki, A. Pike, and S. T. Lindley.
2014. Life cycle modeling framework for Sacramento River winter-run Chinook salmon. NOAA Tech. Memo. NMFS-SWFSC-530, 26 p. [Available at website.]

Hilborn, R., and C. J. Walters.
1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty, 570 p. Chapman & Hall, New York.

Johnson, J. K.
1990. Regional overview of coded wire tagging of anadromous salmon and steelhead in northwest America. Am. Fish. Soc. Symp. 7:782–816.

Lapi, L., M. Hamer, and B. Johnson.
1990. Data organization and coding for a coastwide mark–recovery data system. Am. Fish. Soc. Symp. **7**:720–724.

Lindley, S. T., C. B. Grimes, M. S. Mohr, W. Peterson, J. Stein, J. T. Anderson, L. W. Botsford, D. L. Bottom, C. A. Busack, T. K. Collier, J. Ferguson, J. C. Garza, A. M. Grover, D. G. Hankin, R. G. Kope, P. W. Lawson, A. Low, R. B. MacFarlane, K. Moore, M. Palmer-Zwahlen, F. B. Schwing, J. Smith, C. Tracy, R. Webb, B. K. Wells, and T. H. Williams.
2009. What caused the Sacramento River fall Chinook stock collapse? NOAA Tech. Memo. NMFS-SWFSC-447, 61 p. [Available at website.]

Milner, G. B., D. J. Teel, F. M. Utter, and G. A. Winans.
1985. A genetic method of stock identification in mixed populations of Pacific salmon, *Oncorhynchus* spp. Mar. Fish. Rev. 47(1):1–8.

Myers, J. M., R. G. Kope, G. J. Bryant, D. Teel, L. J. Lierheimer, T. C. Wainwright, W. S. Grant, W. F. Waknitz, K. Neely, S. T. Lindley, and R. S. Waples.
1998. Status review of Chinook salmon from Washington, Idaho, Oregon, and California. NOAA Tech. Memo. NMFS-NWFSC-35, 443 p. [Available at website.]

Nandor, G. F., J. R. Longwill, and D. L. Webb.
2010. Overview of the coded wire tag program in the greater Pacific region of North America. *In* PNAMP special publication: tagging, telemetry and marking measures for monitoring fish populations—a compendium of new and recent science for use in informing technique and decision modalities (K. Wolf and J. O'Neal, eds.), p. 5–46. Pacific Northwest Aquatic Monitoring Partnership Spec. Publ. 2010-002. [Available at website.]

O'Farrell, M. R., S. D. Allen, and M. S. Mohr.
2012b. The Winter-Run Harvest Model (WRHM). NOAA Tech. Memo. NMFS-SWFSC-489, 17 p. [Available at website.]

O'Farrell, M. R., M. S. Mohr, A. M. Grover, and W. H. Satterthwaite.
2012a. Sacramento River winter Chinook cohort reconstruction: analysis of ocean fishery impacts. NOAA Tech. Memo. NMFS-SWFSC-491, 68 p. [Available at website.]

O'Farrell, M. R., M. S. Mohr, M. L. Palmer-Zwahlen, and A. M. Grover.
2013. The Sacramento Index (SI). NOAA Tech. Memo. NMFS-SWFSC-512, 36 p. [Available at website.]

Prager, M. H., and M. S. Mohr.
2001. The harvest rate model for Klamath River fall Chinook salmon, with management applications and comments on model development and documentation. N. Am. J. Fish. Manage. 21:533–547.

Quinn, T. J., and R. B. Deriso.
1999. Quantitative fish dynamics, 560 p. Oxford Univ. Press, New York.

R Core Team.
2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from website, accessed April 2013.]

Restrepo, V. R., and J. E. Powers.
1999. Precautionary control rules in US fisheries management: specification and performance. ICES J. Mar. Sci. 56:846–852.

Satterthwaite, W. H., M. S. Mohr, M. R. O'Farrell, E. C. Anderson, M. A. Banks, S. J. Bates, M. R. Bellinger, L. A. Borgerson, E. D. Crandall, J. C. Garza, B. J. Kormos, P. W. Lawson, and M. L. Palmer-Zwahlen.
2014. Use of genetic stock identification data for comparison of the ocean spatial distribution, size at age, and fishery exposure of an untagged stock and its indicator: California Coastal versus Klamath River Chinook Salmon. Trans. Am. Fish. Soc. 143:117–133.

Satterthwaite, W. H., M. S. Mohr, M. R. O'Farrell, and B. K. Wells.
2013. A comparison of temporal patterns in ocean spatial distribution of California's Central Valley Chinook salmon runs. Can. J. Fish. Aquat. Sci. 70:574–584.

Winship, A. J., M. R. O'Farrell, and M. S. Mohr.
2014. Fishery and hatchery effects on an endangered salmon population with low productivity. Trans. Am. Fish. Soc. 143:957–971.

Weitkamp, L. A., and K. Neely.
2002. Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. Can. J. Fish. Aquat. Sci. 59:1100–1115.

Yoshiyama, R. M., F. W. Fisher, and P. B. Moyle.
1998. Historical abundance and decline of Chinook salmon in the Central Valley region of California. N. Am. J. Fish. Manage. 18:487–521.

Zar, J. H.
1999. Biostatistical analysis, 4th ed., 663 p. Prentice-Hall, NJ.

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  Using the recruitment model, estimates of age-1 recruitment were determined. [Estimates did not use the recruitment model.]
  Correct:
  Using the recruitment model, we determined age-1 estimates of recruitment. [The participle now modifies the word *we,* i.e., those who were using the model.]
  Incorrect:
  Based on the collected data, we concluded that the mortality rate for these fish had increased. [*We* were not based on the collected data.]
  Correct:
  We concluded on the basis of the collected data that the mortality rate for these fish had increased. [Eliminate the participle and replace it with an adverbial phrase.]

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